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Effects of an Exotic Plant Invasion on Arthropod Assemblages

A dissertation submitted in partial satisfaction of the

requirements for the degree Doctor of Philosophy

in Ecology, Evolution and Marine Biology

by

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ABSTRACT

Effects of an Exotic Plant Invasion on Arthropod Assemblages

by

Denise Anne Knapp

Invertebrate responses to plant invasions can help delineate the drivers of biodiversity and community patterns, thus guiding the conservation and restoration of diverse native ecosystems. Although it is well known that invasive species have pervasive effects on native communities and ecosystems, our knowledge of the relative contributions of, and interactions among, key factors determining invader impacts is limited. Among potentially key factors is invader abundance, but few studies have examined its relationship to community structure. Those studies have shown varying relationships between invertebrate assemblages and invader cover, illustrating the need for additional studies on the forms and mechanisms of relationships between invertebrate biodiversity and invasive plant abundance.

For my dissertation work, I asked what effect non-native plant invasions are having on entire arthropod assemblages, and how that effect is related to the degree of invasion. I further asked how the responses by component feeding guilds contribute to these relationships. I answered these questions by conducting a meta-analysis and review of

existing studies, then investigating the effects of one invader, *Carpobrotus edulis*, on coastal dune arthropods at four different coastal California sites. At Vandenberg Air Force Base, Montaña de Oro State Park, and San Buenaventura State Beach, I utilized unmanipulated *Carpobrotus* populations to compare paired invaded and uninvaded patches and to investigate a gradient of *Carpobrotus* infestation. At Coal Oil Point Reserve, I conducted an experimental restoration trial, removing varying amounts of *Carpobrotus* and re-vegetating with native dune plants.

The meta-analysis showed negative effects of non-native plant invasions on arthropod richness, which are in part determined by the abundance of the invader, and are greatest at high levels of invader abundance (70% cover or greater). My field research showed that these effects vary by site, season, and sampling technique/stratum, and are apparently modulated by the characteristics of both the invader and the invasion itself, including growth patterns, litter production, invader abundance, and native plant diversity. Even a relatively small amount of *Carpobrotus edulis* has negative effects on arthropod abundance, richness, and composition, with an exponential decrease in abundance and richness and a shift in composition well before 50% *Carpobrotus* cover. Changes in feeding guilds and composition helped to suggest the drivers of these patterns, and revealed a particularly strong effect on fossorial arthropods, likely related to the dense rooting structure of *Carpobrotus*. Thus, while the negative effects of non-native plant invasions typically increase with increasing invader cover, the form of this relationship is determined by the attributes of both the invader and the invaded system.

INTRODUCTION

Exotic plant invasions are a major element of global environmental change (Vitousek et al. 1997; Mack et al. 2000; Sala et al. 2000). Invasive non-native plants alter disturbance regimes, nutrient cycles, the physical environment, fluxes of both materials and energy, and reduce native biodiversity (Wilcove et al. 1998; Mack and D'Antonio 1998; Liao et al. 2008; Gaertner et al. 2009; Ehrenfeld 2010; Bezemer et al. 2014). Invertebrates such as arthropods are excellent indicators of the consequences of plant invasions, because they play key roles in nutrient recycling, pollination, seed dispersal, energy flow, and structuring plant and animal communities (Gullan & Cranston 2005). They also respond quickly, sensitively, and locally to environmental changes (Kremen et al. 1993). Analysis of invertebrate responses to plant invasions can help delineate the drivers of biodiversity and community patterns, thus guiding the conservation and restoration of diverse native ecosystems (Lodge 1993; McMahon et al. 2006).

Attributes that Determine Invader Impacts on Native Communities

Although it is well known that invasive species have pervasive effects on native communities and ecosystems, our knowledge of the relative contributions of, and interactions among, key factors determining invader impacts is limited (Thomsen et al. 2011). Among potentially key factors is invader abundance, but few studies have examined relationships between this attribute and community structure (e.g., Parker et al. 1999; Ricciardi 2003; Thiele et al. 2010). Authors that have investigated invertebrate richness and

invader cover have reported varying relationships, including negative monotonic, asymptotic, or exponential (Slobodchikoff and Doyen 1977; Heleno et al. 2009; Schooler et al. 2009; Litt and Steidl 2010; Spyreas et al. 2010), and one recent study found that insect herbivore richness peaked at intermediate levels of invasive grass cover (Almeida-Neto et al. 2011). These varied results illustrate the need for additional studies on the forms and mechanisms of relationships between invertebrate biodiversity and invasive plant abundance, and challenge the assumption that per-capita invasive plant impacts are constant (Parker et al. 1999).

Variability in the form of relationships between invertebrate communities and plant invader abundance likely results from differences in not only the characteristics of the invader, but also the traits of the species affected (e.g., trophic level, habitat, specialization), as well as environmental and biological conditions in the invaded community (Gaertner et al. 2009; Magee et al. 2010; Almeida-Neto et al. 2011; Thiele et al. 2010; Thomsen et al. 2011). For example, invaders alter ecosystem processes (including hydrological routing, soil stability, and nutrient cycling) with many repercussions for native communities (Vitousek 1990, Magee et al. 2010). Invasive plant species with greater phylogenetic distance to resident native species can be underutilized by invertebrate consumers (Strong et al. 1984; Harvey et al. 2012). Further, several studies have linked declines in arthropod or bird abundance and diversity to decreasing plant diversity (e.g., Schooler et al. 2009; Spyreas et al. 2010; Almeida-Neto et al. 2011) and structural complexity (Brose 2003; Langellotto and Denno 2004).

Although there is some evidence that non-native plant invasions have negative effects on arthropods (e.g., Dibble et al. 2013, van Hengstum et al. 2014), most studies have concentrated on a limited number of arthropod species, with few considering the impacts of plant invasions on entire arthropod assemblages containing species with many functional and trophic roles (Bezemer et al. 2014). An analysis of invasive plant impacts on all arthropod groups will suggest the mechanisms for the effects of plant invasions on entire communities, a first step in linking invasion impacts on community structure to ecosystem processes (Levine and D'Antonio 2003).

Among arthropod feeding guilds, herbivores (particularly specialized herbivores) are often most negatively affected by introduced plants, because they have adapted to tolerate the chemical and physical defenses of native plants (Schoonhoven 1972; Mattson 1980; Bernays and Graham 1988; Kappes et al. 2007; Proches et al. 2008; Hartley et al. 2010). Predators and parasitoids can decline as invasive plants reduce native plant biodiversity, as they benefit from a greater diversity and complexity of plants and habitats which provide them with a greater abundance and diversity of prey, hosts, alternative food resources, perch sites, and refuges (Langellotto and Denno 2004; Scherber et al. 2010; Price et al. 2011). These effects may be attenuated with increasing trophic level, however, ultimately resulting in weak effects of invasions on parasitoid and predator abundance and richness (Scherber et al. 2010). Because pollinators vary greatly in their specialization for specific plants (Johnson and Steiner 2000), their abundances can either increase, as generalists

track the often large, abundant, and showy flowers of invaders (Traveset and Richardson 2006, Bjerknes et al. 2007) or can decrease, as invasive plants reduce the diversity of native plants used by specialists (Valtonen et al. 2006; Moron et al. 2009). Finally, detritivores may benefit from the high biomass production of invasive plants (Liao et al. 2008; Grotkopp et al. 2010), which produce copious amounts of litter accumulating over successive growth cycles (Holdredge and Bertness 2011; Topp et al. 2008; Moron et al. 2009). On the other hand, detritivore diets may be more specialized than commonly thought (Wolkovitch et al. 2009), which would result in negative impacts by plant invaders.

Dunes and *Carpobrotus*

Coastal dunes in California support unique plant and insect communities (Powell 1978[81]; Rundel and Gustafson 2005), but have been greatly altered by human activities, such as development, recreation, and sand mining (Holland and Keil 1990; Pickart and Barbour 2007). Most California dunes now support a higher cover and relative abundance of exotic than native plant species, with native plants dominating in less than half of the total dune area (Pickart and Barbour 2007).

Hottentot fig or highway iceplant (*Carpobrotus edulis*) was introduced to California in the early 1900's for soil stabilization, and now is found in coastal habitats along the entire California coastline (Albert 2000). Owing to its dense, fibrous roots, mat-like growth, and high biomass production (D'Antonio and Mahall 1991, Molinari et al. 2007), *Carpobrotus*

edulis stabilizes highly mobile coastal dunes, suppresses the growth of native plants, and generates an accumulation of both living and dead organic matter (D'Antonio 1993; Albert 1995, 2000; Campos et al. 2004; Vila et al. 2006; Molinari et al. 2007). It also produces abundant flowers and pollen (Vila et al. 1998, Moragues and Traveset 2005). Lastly, *Carpobrotus* is phylogenetically distinct because only one native member of its family, the Aizoaceae, occurs in coastal California (Hickman 1993). All of these characteristics, which result in substantial ecosystem-level alteration, are likely to cause altered arthropod assemblages, however these impacts are largely unknown.

Dissertation Overview

My doctoral research addresses the questions of how arthropod abundance, richness, composition, and feeding guilds (collectively, "arthropod assemblages") respond to invasions by non-native plant species. In Chapter 1, I present the results of a meta-analysis of the effects of plant invasions on invertebrate richness and diversity, and show that plant invaders are significantly reducing both of these attributes. As part of this meta-analysis, I evaluate the effects of invader abundance (cover) and time since invader establishment on arthropod diversity. I show that negative effects tend to decrease as time since establishment increases, and increase as invader cover class increases, with a threshold around 70% cover after which effects are strongest. In Chapter 1 I also present a literature review of arthropod feeding guild responses to plant invasions, and show that specialists and pollinators are most negatively affected by plant invasions.

In Chapter 2, I compare arthropod assemblage structure both between paired invaded and uninvaded patches and along a gradient of *Carpobrotus edulis* cover at three coastal California dune sites. I show that while there is a strong negative effect of *Carpobrotus* on overall arthropod richness, relationships between arthropod variables and *Carpobrotus* depend strongly on site, season, and arthropod subgroup/sampling technique. Furthermore, it appears that strong impacts are occurring with even a small degree of *Carpobrotus* invasion. These findings are corroborated in Chapter 3, in which I present the results of a restoration experiment designed to test the responses of arthropod assemblages to varying degrees of *Carpobrotus* and native plant cover at Coal Oil Point Reserve. I show that arthropod abundance decreases exponentially with increasing *Carpobrotus* cover for most taxa. Fossorial detritivore and predator taxa are most negatively affected, perhaps due to dense *Carpobrotus* roots which extend beyond the above-ground canopy and pose a barrier. Aerial detritivores and thrips respond positively to *Carpobrotus* invasion, associated with the abundant plant litter and large showy flowers that it produces. My results indicate that for the most part, arthropod communities converge to natural configurations within a few years following *Carpobrotus* removal.

My research shows that a plant invader's per capita effects can vary with the degree of invasion. The relationship between an invader's abundance and the associated arthropods is mediated by its effects on plant assemblages, the recipient arthropod community, and the characteristics of the invader itself. In the case of *Carpobrotus*, its dense fibrous root

system appears to be making the below-ground environment less favorable for many soil-dwelling invertebrates, while its dense plant litter is favoring above-ground detritivores, particularly flies. While its taxonomic isolation from the native flora of California may be driving a negative response by many specialist herbivores, its long residence time on the central coast of California also appears to have facilitated utilization at some sites by other herbivores, including several specialists. Predators and parasitoids in turn appear to be responding to changes in their host populations. Lastly, pollinators can be both positively and negatively affected, depending on *Carpobrotus* abundance at local and landscape scales, the associated native plant diversity and abundance, and the specialization level of the pollinator taxa involved.

A quantitative understanding of the relationships between invader abundance and impacts on native communities will enable policy makers and land managers to set restoration targets and prioritize management practices (Byers et al. 2002; Andreu et al. 2009). The magnitude and patterns of invasive plant impacts on arthropod abundance, diversity, and community structure can help to determine appropriate levels of invasive plant control and native plant re-establishment, by indicating how biodiversity can be maximized (Le Maitre et al. 2011). My field research has shown, for example, that even small amounts of *Carpobrotus edulis* can greatly reduce dune arthropod abundance and richness, therefore this species should be a high priority for removal at any level of invasion. More generally, this study has provided data for the effects of an invasive species on native communities,

contributing to a worldwide database on native biodiversity responses to rapidly changing environments (Hillebrand et al. 2008).

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CHAPTER 1

EFFECTS OF PLANT INVASIONS ON INVERTEBRATE DIVERSITY AND FEEDING GUILDS: A META-ANALYSIS AND REVIEW

ABSTRACT: Exotic plant invasions are a major ongoing component of global environmental change. Invertebrates can be effective indicators of the consequences of these invasions owing to their functional roles in ecosystem dynamics. A meta-analysis of plant invasion effects on invertebrate diversity was conducted at two spatial scales, incorporating invader cover and time since establishment as two mechanisms potentially responsible for these effects. These results were combined with a review of published information on richness responses to plant invasions by feeding guild to examine general patterns of impacts. Invertebrate species richness was 31% lower in areas dominated by exotic plants than in areas dominated by native plants. With diversity indices that consider relative abundances, invertebrate diversity was 14% lower. Negative effects tended to decrease as time since establishment increased, and increase as invader cover class increased, with a threshold around 70% cover after which effects were strongest. Among feeding guilds, only pollinators showed a consistent (negative) response. The increased plant litter associated with plant invasions only resulted in increased detritivore richness in half the studies. Restored plots were more species rich than intact native plots relative to invaded plots, perhaps in response to higher plant richness and cover. These results show that plant invaders are negatively impacting invertebrate biodiversity, and that these effects can be partially predicted by the stage of invasion. They also indicate that varying responses by

different feeding guilds are modulating the overall effect of plant invaders on invertebrate biodiversity.

INTRODUCTION

Non-native plant invasions (plants introduced into a new range where they proliferate and spread) are a major ongoing element of global environmental change (Vitousek et al. 1997, Mack et al. 2000; Sala et al. 2000). Plant invaders are key sources of native biodiversity decline (Wilcove et al. 1998; Gaertner et al. 2009; Bezemer et al. 2014), and their alterations of disturbance regimes, nutrient cycling, and fluxes of materials and energy affect ecosystem structure and function (Mack and D'Antonio 1998, Liao et al. 2008, Ehrenfeld 2010). Invertebrates such as arthropods are effective indicators of the consequences of these invasions, because they participate in ecosystem processes such as nutrient recycling, pollination, seed dispersal, energy flow, and the maintenance of plant and animal community structure (Gullan & Cranston 2005). Furthermore, analysis of invertebrate responses to plant invasions can help to delineate the drivers of biodiversity and community patterns, and guide the management and restoration of those systems (Lodge 1993; McMahon et al. 2006). In this paper, I present the results of a meta-analysis and literature review investigating the effects of plant invasions on invertebrate diversity and feeding guilds, and the mechanisms that may be responsible for these effects.

The abundance of a plant invader in a given area is likely a key determinant of its impact on invertebrate diversity (Parker et al. 1999), yet the nature of this relationship is unclear (Ehrenfeld 2010). Although several authors have reported a negative relationship

between invader cover and invertebrate richness (Heleno et al. 2009; Schooler et al. 2009; Litt and Steidl 2010; Spyreas et al. 2010), for example, a recent study found that insect herbivore richness peaked at intermediate levels of invasive grass cover, which they found to be related to host plant richness (Almeida-Neto et al. 2011). Similarly, Van Riper et al. (2008) found that riparian bird diversity was greatest at intermediate densities of invasive salt cedar (*Tamarix*), where they observed plant structural diversity to be greatest. The data of both Almeida-Neto et al. (2011) and van Riper et al. (2008) indicate a threshold around 40-60% invader cover above which diversity declines. If such a threshold is common, this information will aid land managers in planning and prioritizing restoration activities (Byers et al. 2002).

A novel plant species may be avoided by insect herbivores because of differences from native plants in characteristics such as nutritional quality, chemical composition, and architecture (Strong et al. 1984; Kuhnle and Muller 2009; Carvalheiro et al. 2010). Even a plant that can be eaten may be avoided when it is not recognized as a food source (Lankau et al. 2004). The number of different herbivores using a novel plant tends to increase with the invader's time since establishment as these physical and behavioral barriers diminish (Kennedy and Southwood 1984; Leather 1986; Brandle et al. 2008; Harvey et al. 2013). Little information exists for the effect of time since establishment on whole arthropod assemblages containing multiple feeding guilds, however. It may be that time since establishment is not critical to higher trophic levels such as predators and parasitoids, which are less directly affected by the plants than herbivores (Scherber et al. 2010). Or

perhaps, time since establishment is still important, via delayed colonization by specialists, as well as behavioral barriers.

Experimentally manipulating the relative abundance of invasive and native plants through species removals and additions is one way to investigate the effects of plant invasions. Such restoration sites might differ in vegetation cover, stature, and diversity from intact remnants, however (depending on time since re-vegetation, disturbance levels, objectives, and techniques), and these differences are certain to affect arthropod communities. Restoration ecologists have given more consideration to invertebrates in recent years (e.g., Ormerod 2003, Dibble et al. 2013), providing multiple studies comparing their assemblages in invaded and re-vegetated areas. These data provide an opportunity to not only learn more about the effects of plant introductions, but also to learn how re-vegetated sites compare to intact native remnants in terms of invertebrate diversity.

In the first part of this chapter, I present the results of a meta-analysis conducted to determine the overall effect of plant invaders on invertebrate richness and other diversity indices, and to investigate several likely drivers of that impact. I asked the following questions: (1) How do plant invasions affect invertebrate richness and diversity? (2) Is the relationship between invertebrate richness and invasive plants influenced by invasive plant cover? (3) Is the relationship between invertebrate richness and invasive plants influenced by the time since establishment of the invasive plant? (4) Does invertebrate richness differ between restored and intact habitats compared to invaded areas? I had the following hypotheses: 1) There is an overall negative effect of plant invasions on invertebrate

richness; 2) This effect becomes stronger with increasing invader cover, with impacts particularly severe over 50% cover, when the exotic plant becomes the dominant species; 3) The negative effects diminish with time since establishment of the invader; 4) Intact native areas support more invertebrate species than restored areas, the latter of which would have had less time for habitat to mature and species to accumulate.

I investigate the effect of time since invader establishment on invertebrate diversity at two spatial scales. Study scale has a strong influence on invertebrate responses to environmental conditions, as taxa have different home range sizes and dispersal abilities (Schieg 2000; Janssen et al. 2009; Larrivee and Buddle 2010). Furthermore, time since invader establishment is positively correlated with range size (Williamson et al. 2009), which itself is strongly and positively related to insect richness (Strong et al. 1984). For the local scale, I consider the length of time the invader resided at a specific location (city, reserve, etc.), whereas for the regional scale I consider its time since establishment within an area hundreds of square kilometers.

The response of invertebrate diversity to plant invasions will also likely vary across invertebrate feeding guilds, because different invaders will have different effects on invertebrate food resources such as native plants, invertebrate prey, and leaf litter, and because these guilds vary in their levels of specialization (Bernays and Graham 1988; Price et al. 2011; Welch et al. 2012). In the second portion of this chapter, I conducted a literature review to investigate responses by five feeding guilds to plant invasion, as there

were insufficient studies containing the data necessary for a meta-analysis. These guilds included herbivores, parasitoids, predators, detritivores, and pollinators.

Individual studies that have compared the species richness responses of different feeding guilds to plant invaders have shown that herbivores, particularly specialists, can be more negatively affected by plant invasions than other feeding guilds, and reflect changes in plant diversity (Kappes et al. 2007; Proches et al. 2008; Almeida-Neto et al. 2011). In turn parasitoids, which are more specialized to their hosts than predators (Price et al. 2011, Welch et al. 2012), benefit from a greater diversity of prey. Because the effects of plant diversity dampen with increasing trophic level, however, predators as well as parasitoids are less affected by changes in plant diversity than herbivores (Scherber et al. 2010). Detritivores, on the other hand, may benefit from the dense plant litter produced by many plant invaders (Holdredge and Bertness 2011; Topp et al. 2008; Moron et al. 2009) if they are typically generalists as suggested by Srivastava et al. (2009). Lastly, pollinators, which utilize plant resources (nectar and pollen) directly and include both specialists and generalists (Johnson and Steiner 2000), may, like herbivores, be more negatively affected by the decreases in plant diversity commonly associated with plant invasions.

Given the above, I hypothesized that herbivore and pollinator richness would be most negatively affected by plant invasions, as these groups utilize plants most directly, but that detritivore richness would increase in response to elevated plant litter. I expected that predators and parasitoids would be least affected, as they are primarily affected indirectly via their host taxa.

METHODS

I compiled studies through both database queries and subsequent surveys of the references cited in compiled papers. ISI Web of Science was searched in November 2012, using the search string: "Topic = (invasive OR exotic AND plant) AND Topic = (arthropod* OR insect* OR invertebrate*). From these searches I assembled 106 published studies, including dissertations, which compared insect, arthropod, or other invertebrate diversity (including richness and other diversity indices, analyzed separately) in invaded versus native habitats. The analysis was restricted to studies which reported means, variances, and sample sizes, and was weighted inversely to the variances in order to give the most accurate estimate of overall effect size (Rosenberg 2000) I extracted the data directly from tables or from graphs using the program DigitizeIt v. 1.5 (I. Bormann, Braunschweig, Germany: http://www.digitizeit.de).

I used the response ratio as an estimator of effect size; in this case, the natural log of the ratio $[X_{exotic}/X_{native}]$, where X represents the mean of either invertebrate species richness or diversity index (analyzed separately) for a given study in either the 'exotic' dominated or the 'native' dominated locations. I chose the response ratio for several reasons: first, I am interested in the magnitude of the relative difference in arthropod diversity between exotic and native vegetation; second, use of the logarithm ensures that deviations these two variables are treated equally (Hedges et al. 1999). Lastly, it allowed me to assess both the model and residual variation, giving an estimate of the importance of the variables analyzed here.

Fifty-four studies met these criteria and were included in my meta-analysis (Table 1). These studies represent a variety of habitat types throughout the world, ranging from grassland to scrub to riparian (Table 1). Fifty-two of these studies reported invertebrate richness (not accounting for the effects of abundance through rarefaction), and fifteen studies reported values for diversity indices incorporating evenness, with 12 reporting results for the Shannon index, two for the Simpson's index, and one for Fisher's alpha. Insects were the focus of 26 studies, 16 reported results for entire arthropod assemblages, and 12 studies described results for other invertebrate groups.

I extracted descriptor variables, where available, from each study, including latitude, time since establishment of the non-native plant at the local (study site) and/or regional (hundreds of square kilometers) scale, invader cover, scale of the study (plant or community), and whether the native-dominated site was intact or restored habitat. Where time since establishment was not reported for a given study, I obtained this information from other sources where possible. In order to utilize the studies which reported cover classes or ranges rather than exact values (over half of them), I placed invader cover into six cover classes. I used natural breaks in the data to develop the following classes: <10%, 10-30%, 30-50%, 50-70%, 70-90%, and >90%. Cover was thus considered 'absolute' and not relative. Studies reporting that the invasive plant "formed a monoculture", was "dense and continuous," or "completely dominated the landscape" were conservatively classified into the 70-90% group. I justify this decision by the finding that model results were not changed by reclassifying these into either 50-70% or 90-100% cover.

I calculated a single effect size per study by averaging data collected over multiple years or seasons. However, when invertebrate richness or diversity in one area dominated by native plants was compared to those in multiple invaded areas or vice versa, I calculated separate effect sizes for each comparison. When studies included multiple levels of descriptor variables (e.g, two or more establishment times or novel plant covers), I calculated an average effect size to determine the overall effect of invasion (vs. native control plant communities), but calculated separate effect sizes for each level of the descriptor variables when analyzing the effects of these descriptor variables on invertebrate richness or diversity.

I performed meta-analyses using the *metafor* (Viechtbauer 2010) package for R 2.15.0. I used random effects models to calculate overall effect sizes for invertebrate richness and diversity (Viechtbauer 2010, Gurevitch & Hedges 1999). To estimate the variation in the effect size described by different variables (cover, study scale, and type of control plot), I used mixed-effects models using the Q statistic. This analysis treats the variables as fixed but includes a random variance component to account for variability across studies. In one case (invader cover), I also report results from a fixed-effects model, which restricts my inferences to the studies examined. For continuous descriptor variables (latitude, invader time since establishment) I used weighted generalized least squares regression to test their relationships with effect size.

After accounting for the variation attributable to descriptor variables, I estimated residual variation (τ^2) using a restricted maximum likelihood estimator (Viechtbauer 2005).

For studies which reported results for all descriptor variable groups (22), I used the Akaike information criterion (AIC) to determine the model that best fit the data.

RESULTS

Invertebrate species richness was 31% lower in areas dominated by exotic plants than in areas dominated by native plants (effect size = -0.37 ± 0.10; Z = -5.48, $p < 0.01$; Fig. 1), but there was significant heterogeneity in the data ($Q_T = 111$, $p<0.0001$). Invertebrate diversity indices were 14% lower with invasion (effect size = -0.15 ± 0.10; Z = -3.42, $p < 0.01$), with low heterogeneity in the data ($Q_T = 13$, $p > 0.50$).

The absolute value of latitude did not explain a significant amount of heterogeneity in effect sizes for species richness ($Q_M = 1.09$, *p = 0.30*), nor did study scale ($Q_M = 0.06$, p = 0.97). Invaded sites had lower invertebrate richness compared to intact native plots as the control (-0.35 ± 0.07; Z = -5.02, $p < 0.01$), and there was a similar trend when plots restored to native species were the control (-0.61 ± 0.17; Z = -1.73, p = 0.08). Effect sizes were thus more negative for the comparisons between invaded and restored sites ($Q_M = 5.1$, p = 0.02; Fig 1).

The negative effects of invasive plants on invertebrate richness were greatest at the shortest local-scale time since establishment and decreased with time, but this pattern was only marginally significant ($Q_M = 3.0$, p =0.08, Fig. 2). On the other hand, time since invader establishment at the regional scale was not related to effect size ($Q_M = 0.40$, $p > 0.50$). The impact of exotic plants on invertebrate species richness tended to increase as invader cover increased (Fig 1), although only cover classes above 70% had confidence intervals

that did not overlap zero. When the cover classes below 70% were combined into a single category, the difference in effect sizes between exotic plant cover classes was marginal in a mixed-model analysis ($Q_B = 4.7$, $p = 0.09$), but the groups were very different when the data were fit to a fixed effects model ($Q_B = 176$, $p < 0.0001$).

In all cases except the models of time since establishment, residual heterogeneity remained significant ($p < 0.01$), indicating substantial amounts of effect size variation that were unexplained by statistical models. The effects of descriptor variables on effect sizes for diversity indices were not analyzed, both because low sample sizes prevented it and because low residual heterogeneity obviated the need for it.

Although there were some effects of descriptor variables on richness effect sizes when the descriptors were considered individually (Figs. 1 and 2), mixed effects models including all descriptor variables at the same time showed no significant (at the $p < 0.05$ level) descriptor effects on response ratios. Between-groups heterogeneity was significant for intact vs. restored plots, ($Q_M = 5.051$, $p = 0.025$), and trended towards significance for the different cover classes ($Q_M = 4.716$, $p = 0.094$). Residual heterogeneity not explained by the single-factor mixed-effects model was significant in all cases.

Herbivores

Among the fifteen studies including data on herbivore richness responses to invasive plants, eight reported a decrease in richness (Kappes et al. 2007; Gerber et al. 2008; Proches et al. 2008; White et al. 2008a; Tallamy and Shropshire 2009; Cameron and Spencer 2010; Harvey et al. 2010; Perre et al. 2011) and seven showed no change in

richness in invaded compared to native habitats (Auerbach and Simberloff 1988; Novotny et al. 2003; Liu et al. 2006; Bito 2007; Zuefle et al. 2008; Rohacova and Drozd 2009; Ando et al. 2010). Of six studies reporting level of specialization, four found that invaders supported fewer specialists (Liu et al. 2006; Bito 2007; Rohacova and Drozd 2009; Novotny et al. 2003). In particular, Novotny et al. (2003) reported a positive relationship between the probability that alien plants were colonized by caterpillar species and the range of host plants used by those species. While Zuefle et al. (2008) and Auerbach & Simberloff (1988) did not find a difference in specialization, Zuefle et al. (2008) noted that their protocol was biased against sampling specialists.

Study scale appears to play a role in these findings. Four of eight studies reporting higher herbivore richness on native than invasive plants sampled invertebrate assemblages at the stand scale (Kappes et al. 2007; Gerber et al. 2008; White et al. 2008a; Cameron and Spencer 2010), whereas all of the studies that did not find significant differences were conducted at the plant scale. In addition, all five of the studies that both found a significant herbivore richness difference between native and exotic plant stands and reported invader cover noted that the alien plant species formed monocultures or dominated plant assemblages (Kappes et al. 2007; Proches et al. 2008; Cameron & Spencer 2010; Harvey et al. 2010; Perre et al. 2011).

Interestingly, Ando et al. (2010) found that several of the most abundant herbivores colonizing alien plants were non-native. Kappes et al. (2007) also mention that an alien slug

utilized invasive *Reynoutria*. The other studies did not address the presence of non-native herbivores, however.

Predators and Parasitoids

The species richness of predators was greater on alien than native plants in two studies (Kappes et al. 2007; Hartley et al. 2010), was lower in two studies (Gerber et al. 2008; Harvey et al. 2010), and was not different in two studies (Proches et al. 2008 [combined with parasitoids]; Hansen et al. 2009). For parasitoids, species richness was lower on exotic than native plant species in three studies (Heleno et al. 2009, 2010; Carvalheiro et al. 2010) and not different in two other studies (Stephens et al. 2006; Proches et al. 2008 [combined with predators]).

Detritivores and Fungivores

Although many studies have found that invertebrate detritivores are more abundant in invaded than native habitats (e.g., Gratton & Denno 2005; Kappes et al. 2007; Topp et al. 2008; Bassett et al. 2011), few studies have examined the effects of plant invasions on detritivore richness. I found five such studies. Two of those (Harvey et al. 2010; Bassett et al. 2011) found more detritivore species associated with non-native than native plants. One study (Gerber et al. 2008) found more detritivore species in native than invaded plots for one habitat type, but no difference in another. Two studies (Proches et al. 2008; Bottollier-Curtet et al. 2011) found no difference in detritivore richness between treatments.

Pollinators

Eight of nine pollinator studies, conducted at a range of scales, reported that pollinator species richness was lower on exotic than native plants (Memmott and Waser 2002; de Groot et al. 2007; Nelson and Wydoski 2008; Moron et al. 2009; Schooler et al. 2009; Florens et al. 2010; Hanula and Horn 2011b; Moranz et al. 2012). The exception was Bartomeus et al. (2008). Whereas generalist taxa such as European honeybees commonly used invasive plants (Memmott and Waser 2002; Parker et al. 2002; Stout et al. 2006; Totland et al. 2006; Lopezaraiza-Mikel et al. 2007; Bartomeus et al. 2010; Woods et al. 2012), it appears that specialist pollinator taxa are those most at risk of decline (Biesmeijer et al. 2006).

DISCUSSION

My analysis revealed 31% lower invertebrate species richness and 14% lower diversity in areas dominated by exotic plants than those dominated by native plants. These studies included a wide range of feeding guilds. While invader cover at classes below 70% had little impact on invertebrate richness, above this threshold the effects were negative. One likely cause of this potential threshold is a decline in diversity of other plant species when an invader comes to dominate (Almeida-Neto et al. 2011). Previous studies have shown that arthropod diversity is positively related to plant species richness, presumably because of effects on structural and food diversity as well as abiotic variables (e.g., temperature, moisture) (Potts et al. 2003, Wolkovitch 2010, Price 2011). Alternatively, exotic plants may be responding positively to a disturbance, such as vegetation clearing or

fragmentation, while invertebrates simultaneously respond negatively to that disturbance. Disturbances can facilitate non-native plant invasions, as they provide establishment opportunities and put native taxa at a disadvantage (Hobbs and Huenneke 1992; Lozon and MacIsaac 1997). They can also be detrimental to arthropod richness (Welch et al. 2012).

Although there was a tendency for invasive plant impacts on invertebrate species richness to decrease with time since invader establishment at a site, this pattern was only marginally significant. Invertebrate assemblages as a whole thus appear to be affected less by time since establishment than insect herbivores (Kennedy and Southwood 1984; Leather 1986; Brandle et al. 2008). This is in accordance with findings that generalist herbivores are likely to accumulate on an introduced plant more quickly than specialists (Andow and Imura 1994). Herbivores also accumulate more rapidly on exotics that are closely related to native plant taxa in the invaded habitat (Connor et al. 1980; Auerbach and Simberloff 1988; Dawson et al. 2009), perhaps weakening the pattern found for introduced taxa overall.

My analysis showed that restored plots contained more invertebrate species than intact native plots relative to invaded plots, but with greater variability. Flower visitors can be more diverse at restoration than reference sites, even after $\leq$ one year (Waltz & Covington 2004; Kaiser-Bunbury et al. 2009; Lomov et al. 2010). Early-colonizing invertebrates such as adult butterflies can be attracted to more open, sunny restored areas disturbed by earth moving, invasive plant removal, and outplanting (Magoba and Samways 2010; Hanula and Horn 2011a; Samways et al. 2011). Florens et al. (2010), for example,

found that butterfly richness decreased as percent plant cover rose. Alternatively, higher invertebrate richness in restored than intact native areas could be the result of higher plant richness and cover in restored than remnant intact habitats, which would provide more food resources (Hanula and Horn 2011a).

The high residual heterogeneity in richness after incorporating the effects of invasive plants and other descriptor variables indicates that other unmeasured factors are important in driving invertebrate richness or diversity patterns. To some degree, these other factors, including habitat and food variables, may be revealed by a separate analysis of different feeding guilds, including herbivores, predators and parasitoids, detritivores, and pollinators.

Herbivores

In my review only slightly more than half of the studies addressing herbivore richness as a whole reported a negative effect of exotic plant species. It is of interest that a few studies (Kappes et al. 2007; Ando et al. 2010) noted non-native herbivores colonizing the alien plant, which may be tempering the richness response as a whole. Similarly, Ulyshen et al. (2010) noted than a non-native herbivore dominated the beetle community using invasive Chinese privet (*Ligustrum sinense*) in floodplain forests.

Specialist herbivores were slightly more negatively affected than herbivores as a whole, with four of the six studies that investigated level of specialization finding that alien plants hosted a greater proportion of generalist than specialist herbivore species.

Specialists can only tolerate the chemical and physical defenses of specific plants to which they have adapted (Schoonhoven 1972; Mattson 1980; Bernays and Graham 1988).

Stand-scale comparisons were far more likely to find that exotic plant species had a negative effect on herbivores. The plant-scale studies censused herbivores on both native and exotic plants, including exotic plants which were congeneric with native plants. As a consequence, the nearby presence of a native plant may have increased the likelihood that associated specialist herbivores also used congeneric introduced plants (Graves and Shapiro 2003; Roques et al. 2006). These plant-scale studies did not report data on the cover of the alien plant species. In contrast, the stand-scale studies focused on habitat changes caused by plant invaders, and were more likely to investigate invaders that had become dominant in the system, which likely explains the more negative effect found at that scale.

Predators and Parasitoids

My review revealed equivocal relationships between predator and parasitoid richness and invasive plants, with nearly equal numbers finding lower and higher species richness in invaded habitats. Natural enemies as a whole respond positively to the abundance and diversity of their herbivore prey which, in turn, are related to the abundance and diversity of host plants (Siemann et al. 1998; Memmott et al. 2000; Petermann et al. 2010; Scherber et al. 2010; Wimp et al. 2010; Ebeling et al. 2012). Natural enemies also rely on vegetation structural and compositional heterogeneity as well as habitat or landscape diversity (Crooks 2002; Brose 2003; Langelotto & Denno 2004; Rand &

Tscharntke 2007; Woodcock et al. 2007; Pearson 2009; Schmidt and Rypstra 2010; Chaplin-Kramer et al. 2011), which provide a refuge from their own predators along with supplementary food such as nectar, pollen, fungi, and plant fluids (Brose 2003; Langelotto & Denno 2004; Price et al. 2011). However, the variable results of the studies compiled here suggest that responses are context- and taxon-specific (e.g. Siemann 1998; Halaj et al. 2000; Koricheva et al. 2000; Schaffers et al. 2008) and that the dampening effect of increasing trophic level (Scherber et al. 2010) is modulating the response by predators and parasitoids.

Detritivores and Fungivores

Areas with high densities of invasive plants often have dense plant litter produced over successive growth cycles (Holdredge and Bertness 2011; Topp et al. 2008; Moron et al. 2009). Inputs of leaf litter are often high due to the rapid growth rates of many invasive species (Grotkopp et al. 2010). Srivastava et al. (2009) suggested that most detritivorous taxa are generalists, and hypothesized that increased litter biomass with plant invasions would result in the increased abundance and richness of invertebrate detritivores. Yet only two of the four studies that I was able to identify showed a consistent positive response by detritivores to plant invasions. It may be that detritivores are responding more to invader-mediated changes in habitat structure or disturbance regime (Ribeiro-Troian et al. 2009; Wolkovitch et al. 2009). Alternatively, detritivores may be more specialized than previously thought, as suggested by Wolkovitch et al. (2009).

Pollinators

I found that pollinator species richness was lower on exotic than native plants in eight of nine studies identified. The negative impact of plant invasions on pollinator richness will likely increase with the cover or abundance of the invasive plant species (Munoz and Cavieres 2008; Morales and Traveset 2009; Flanagan et al. 2010; Dietzsch et al. 2011; Williams et al. 2011) and the degree of overlap between exotic and native species in floral traits such as clustering, color, and shape (Gibson et al. 2012; Thijs et al. 2012). Multiple reviews and meta-analyses have concluded that the presence of invasive plants also has a negative effect on pollinator visitation rates to native plant species flowering at the same time, resulting in a lower seed set of those native species (Bjerknes et al. 2007; Morales and Traveset 2009; Montero-Castano and Vila 2012). The removal of invasive species typically restores pollinator richness to levels found in areas dominated by native plant species (Kaiser-Bunbury et al. 2009; Hanula and Horn 2011a; Pfitsch and Williams 2009; Fiedler et al. 2012).

CONCLUSIONS

This meta-analysis showed that plant invasions are decreasing both the species richness and diversity of invertebrate assemblages. This has implications for the ecosystem services such as pollination, leaf litter breakdown, and efficient nutrient cycling, that invertebrates provide (Hector et al. 2000; Klein et al. 2003; Balvanera et al. 2005; Srivastava et al. 2009; Eisenhauer et al. 2012). My results suggest that these impacts are greatest shortly after invader establishment (< 20 years) and at exotic plant cover greater than 70%.

While a review of effects by feeding guild showed that most had equivocal results, pollinators exhibited a strong tendency for lowered richness. In addition, studies suggest that responses are stronger for invertebrate taxa with a narrower host range, such as specialist herbivores. Furthermore, non-native arthropods appear to readily colonize exotic plants, which could be tempering overall richness effects. A better understanding of the factors leading to negative invader impacts on biodiversity, including time since establishment, invader cover, and feeding guild, will help land managers to pursue practices that minimize the financial costs and maximize the ecological benefits of invader management.

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Appendix 1: Studies used in the meta-analysis and their attributes. "Time?" indicates whether or not time since establishment was reported in the reference, and "Cov?" indicates whether or not cover of the invader was reported.

Reference	Location	Latitude	Habitat	Time?	Cov?	Scale	Control	#Exotics	Richn.	Div.
Ando et al 2010	central Japan	35.07	seminatural	X		plant	native	1	X	
Bailey et al 2001	Arizona, USA	34.67	riparian	X		plant	native	1	X	
Bartomeus et al 2008	Spain	42.32	scrub	X	X	community	native	2	X	
Bassett et al 2012	New Zealand	35.02	lake/ littoral	X	X	plant	intact	1	X	
Bickel & Closs 2009	New Zealand	45.03	lake/ littoral	X		community	restored	1	X	X
Bock 1986	Arizona, USA	31.65	grass/forbland	X	X	community	intact	1	X	
Brandle et al 2008	Germany	51	various			plant	intact	1	X	
Burghardt et al 2009	Pennsylvania, USA	40.25	seminatural			community	intact	1	X	
Cameron & Spencer 2010	Texas, USA	29.53	grass/forbland	X	X	community	intact	1	X	X
Chey 1998	Sabah, Borneo	5.42	forest	X		community	intact	5	X	
Christopher & Cameron 2012	Ohio, USA	39.12	forest		X	community	intact, restored	1		X
Cord 2011	Texas, USA	27.49	grass/forbland	X	X	mixed	intact	1	X	
deGroot et al 2007	Slovenia	46.05	seminatural		X	community	intact	1	X	X
Durst et al 2008	Arizona, USA	33.65	riparian	X	X	community	intact	1	X	X
Florens et al 2010	Mauritius	20.4	forest			community	restored	1	X	
Gerber et al 2008	Switzerland, Germany, & France	47	grass/forbland, scrub	X		community	intact	1		X
Gossner 2006	Germany	48.18	forest	X	X	community	intact	1		X
Gremmen et al 1998	Marion Island, SubAntarctic	46.83	riparian	X	X	community	intact	1	X	
Hagen et al 2010	Robinson Crusoe Island, Chile	33.63	forest	X		community	intact	1	X	
Hanula & Horn 2011a	Georgia, USA	33.88	forest	X	X	community	intact, restored	1	X	X

Hanula & Horn 2011b	Georgia, USA	33.88	forest	X	X		community	intact, restored	1	X	X
Harris et al 2004	New Zealand	41.2	scrub		X		community	intact	1	X	
Hartley et al 2010	Texas, USA	29.53	grass/forbland	X		1	plant	intact	1	X	
Harvey et al 2010	Australia	34	marsh		X		plant	intact	1	X	X
Herrera & Dudley 2003	California, USA	38.23	riparian	X	X		community	intact	1	X	X
Hills et al 2008	Australia	33.82	cave				plant	intact	2	X	
Holmquist et al 2011	California, USA	36.45	desert spring	X			community	intact	1	X	
Hugel 2012	Rodrigues Island, SW Indian Ocean	19.72	forest				community	restored	1	X	
Kappes et al 2007	Germany	51.15	riparian		X		community	intact	1	X	
Magoba & Samways 2010	South Africa	23.02	riparian		X		community	intact, restored	1	X	
Magoba & Samways 2012	South Africa	18.9	scrub		X		community	intact, restored	1	X	
Magura et al 2000	Hungary	48.47	forest	X	X		community	intact	1	X	X
Moron et al 2009	Poland	50.05	grass/forbland	X	X		community	intact	1	X	
Osunkoya et al 2011	Australia	27.83	forest	X	X		community	intact	1	X	X
Parr et al 2010	Australia	12.72	savanna	X	X		community	intact	1	X	
Pinto 1997	Portugal	40.28	riparian				community	intact	2	X	
Pryke & Samways 2009	South Africa	33.95	forest, scrub				community	intact	1	X	
Robertson et al 2011	South Africa	25	savanna, scrub	X	X		community	intact	1	X	
Samways & Sharrat 2010	South Africa	33.55	riparian				community	intact, restored	1	X	
Samways et al 2011	South Africa	33.3	riparian, scrub				community	intact	1	X	
Sax 2002	California, USA	37.88	forest	X			community	intact	1	X	
Schirmel et al 2011	Germany	54.53	dunes	X	X		community	intact	1	X	
Schoeman 2008	South Africa	34.05	scrub	X			community	intact	1	X	
Simao et al 2010	Indiana, USA	39.22	forest	X			community	intact	1	X	
StJohn et al 2006	Kansas, USA	39.1	grass/forbland	X			plant	intact	1	X	

Tallamy & Shropshire 2009	Eastern USA	36.5 to 45	various			plant	intact	1	X	
Talley et al 2012	California, USA	32.75	riparian			plant	intact	1	X	X
Theel et al 2008	Mississippi, USA	33	aquatic			community	intact	1	X	
Triet et al 2004	Vietnam	10.7	grass/forbland	X	X	community	intact	1	X	X
Ulyshen et al 2010	Georgia, USA	33.88	forest	X		community	restored	1	X	
Webb et al 2000	Australia	35.4	dunes	X	X	community	intact	1	X	
White et al 2008	Australia	27.83	grass/forbland	X		community	intact	1	X	
Wu et al 2009	China	31.52	marsh	X	X	mixed	intact	1	X	X
Zuefle et al 2008	Delaware, USA	39.7	seminatural			plant	intact	1	X	

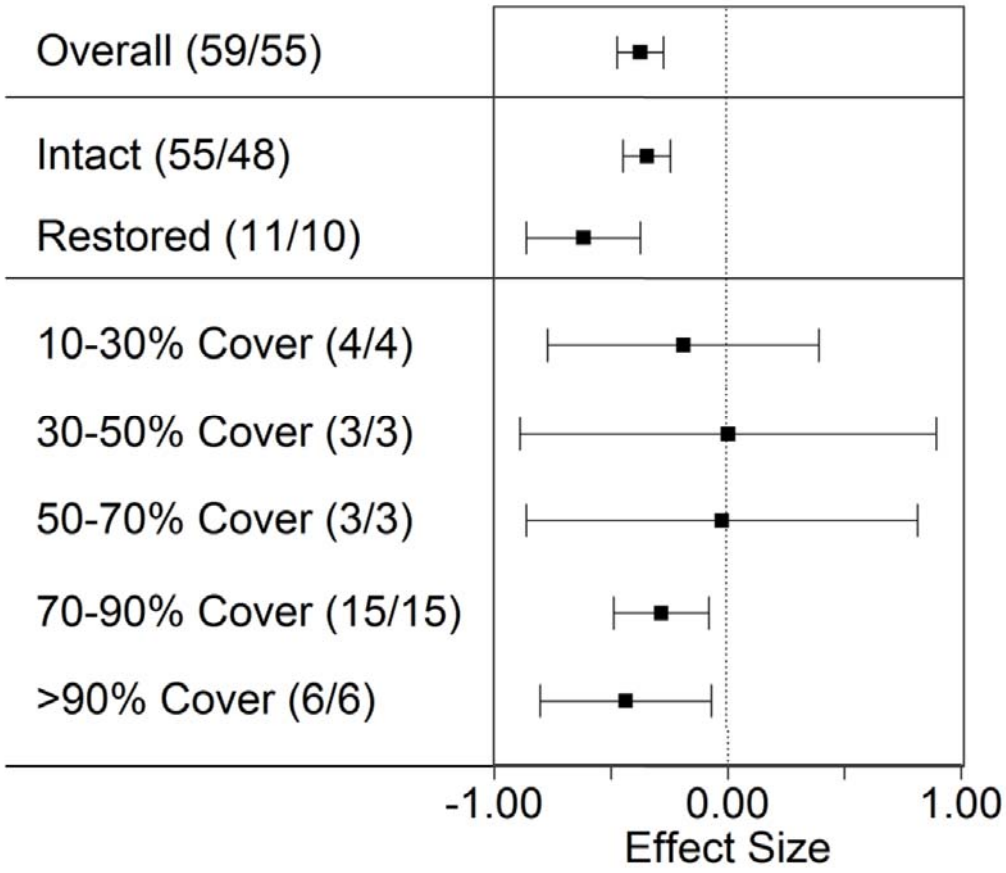

Figure 1: Mean invertebrate richness effect sizes (± 95% confidence limits) across all studies (top panel), as well as between studies contrasting effect sizes where native plots represented restored or intact habitats (middle panel). The bottom panel shows mean richness effect sizes (± 95% confidence limits) for exotic plant cover classes. Numbers in parentheses indicate the number of effect sizes and the total number of studies, respectively.

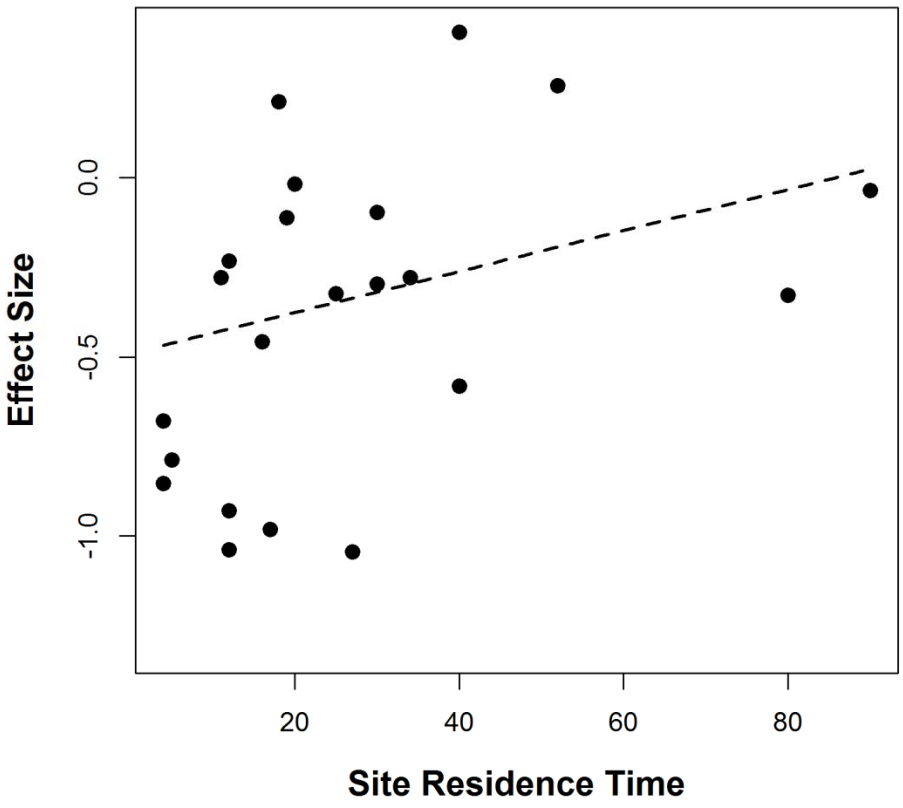

Figure 2: Relationship between effect size for invertebrate richness and time since invader establishment at a site for the 22 studies for which these data were available. Dashes indicate line of best fit.

CHAPTER 2

EFFECTS OF *CARPOBROTUS EDULIS* PRESENCE AND ABUNDANCE ON COASTAL DUNE ARTHROPOD ASSEMBLAGES AT THREE COASTAL CALIFORNIA SITES

Abstract: Few studies have addressed the relationship between plant invader abundance and invertebrate assemblages, particularly across multiple sites, seasons, and feeding guilds. This information can provide insight into the patterns and mechanisms whereby plant invaders impact ecosystem structure and function. Here I examine how the presence and abundance of *Carpobrotus edulis* affects the abundance, species richness, feeding guilds, and composition of coastal dune arthropods, using two approaches: 1) paired invaded and uninvaded patches and 2) a gradient of *Carpobrotus* infestation. Arthropod sampling was conducted in March and June of 2011 using both sand sifting and pan trapping techniques. Relationships between arthropod variables and *Carpobrotus* depended strongly on site and arthropod subgroup/sampling technique. Paired plots revealed a significant negative effect of *Carpobrotus* on overall arthropod richness in three out of four season/method combinations. Arthropod abundance was higher in native than *Carpobrotus* plots in two of four combinations. In contrast to these paired difference values, arthropod responses to increasing *Carpobrotus* cover (regression approach) often differed in sign and strength at the three sites and overall, few significant relationships were found. Sometimes, significant patterns were opposite in different seasons. Omnivores, parasitoids, and pan-trapped predators were all consistently more abundant in

uninvaded plots, but soil predators differed in their responses depending on sampling time. Both soil and pan-trapped detritivores sometimes decreased with increasing *Carpobrotus*, and both herbivores (including just specialist herbivores in the family Cicadellidae) and pollinators exhibited both negative and positive relationships with *Carpobrotus* cover at different sites and times. Effects often varied for different taxa within a feeding guild. Arthropod composition was significantly different between all sites in both seasons, suggesting that the different taxonomic groups at different sites are important influences on these variable responses to *Carpobrotus* invasion. A strong shift in arthropod composition was evident at a *Carpobrotus* cover threshold of 30% in March, while a more gradual but significant change in composition was found in June. Results may have been stronger using a paired plot approach because strong impacts are occurring with any degree of *Carpobrotus* invasion. Therefore although it is appealing to sample an invader across varying levels of invasion, a combination of analyses including evaluation of compositional shifts is likely to yield the most insight into how invader impacts arise.

Introduction

Biological invasions have profoundly affected native biodiversity and the structure and function of ecosystems (Wilcove et al. 1998; Mack and D'Antonio 1998, Liao et al. 2008, Ehrenfeld 2010). One of the ways that plant invasions in particular can affect ecosystems is by altering arthropod assemblages, which in turn influence nutrient recycling, pollination, and the composition and structure of plant and animal communities

(Gullan & Cranston 2005). As a consequence, knowledge of the responses of arthropod communities to plant invasions provides insight into the mechanisms through which plant invaders create impacts and how communities will respond to invader control.

A meta-analysis of published studies has shown that plant invaders generally have a negative effect on invertebrate abundance and richness, although this impact may vary with the abundance of the invader and the amount of time it has been present (van Hengstum et al. 2014; Chapter 1). Effects can also vary by site and season (e.g. Lacan et al. 2010; Osunkoya et al. 2011). Few studies have addressed the relationship between a specific invader's abundance and invertebrate assemblages, particularly across multiple sites, and those have produced varied results. Some relationships have been reported to be negative and linear, such as between insect richness and invasive grass biomass in Arizona grasslands (Litt and Steidl 2010), and between Homopteran insect diversity and *Phalaris arundinacea* cover in Illinois wetlands (Spyreas et al. 2010). In contrast, Almeida-Neto et al. (2011) found a quadratic (hump-shaped) relationship between invertebrate herbivore richness and exotic grass dominance in tropical savannas in Brazil. These varied relationships likely result from differences among invaders in their effect on plant composition, and among the settings in which they invade (Heleno et al. 2009; Simao et al. 2010; Almeida-Neto et al. 2011) including associated habitat structure (Murdoch et al. 1972; Brose 2003; Janssen et al. 2009), and variation in abiotic variables (Menendez et al. 2007). More data are clearly needed to develop a predictive model of plant invader effects on higher trophic levels.

The responses of invertebrate diversity to plant invasions will also likely vary across invertebrate feeding guilds, because these guilds vary in their levels of specialization (Bernays and Graham 1988; Price et al. 2011; Welch et al. 2012) and because different invaders will have different effects on invertebrate food resources, such as native plants, invertebrate prey, and leaf litter (Chapter 1). Further, effects may get weaker as trophic levels increase and plant influences become more indirect (Scherber et al. 2010). To date, however, most studies have not characterized invasive plant impacts on arthropod assemblages across the full array of invertebrate feeding guilds, or the relationship between invasive plant abundance and the abundance of each of these guilds.

This study examines the effects of the presence and abundance of an invasive mat-forming succulent *Carpobrotus edulis* (L.) (highway iceplant, Hottentot fig) on the abundance, species richness, and feeding guilds of coastal dune arthropods. Coastal dunes in California support unique plant and insect communities (Powell 1978[81]; Rundel and Gustafson 2005), but have been greatly altered by human activities, such as development, recreation, and sand mining (Pickart and Barbour 2007). Most dune systems now support a higher cover and relative abundance of naturalized than native vegetation, with native plants dominating in less than half of the total dune area (Pickart and Barbour 2007).

Carpobrotus edulis was introduced to California in the early 1900's for soil stabilization, and now is found in coastal habitats along the entire California coastline (Albert 2000). Owing to its dense, fibrous rooting system, mat-like growth, and high biomass production (D'Antonio and Mahall 1991, Molinari et al. 2007), *Carpobrotus edulis*

stabilizes highly mobile coastal dunes, suppresses the growth of native plants, and generates an accumulation of both living and dead organic matter (D'Antonio 1993; Albert 1995, 2000; Campos et al. 2004; Vila et al. 2006; Molinari et al. 2007). It also produces abundant flowers and pollen, and is visited by an array of pollinators (Vila et al. 1998, Moragues and Traveset 2005).

These impacts likely alter arthropod assemblages, yet little is known about this. For example, herbivore abundance should be reduced due to negative effects on the diversity of plant food sources. Predator and parasitoid abundance should also be reduced associated with plant diversity, because a lower diversity and complexity of plants and habitats provides fewer prey or hosts, as well as perch sites (e.g., Langelotto & Denno 2004; Woodcock et al. 2007). In contrast, *Carpobrotus* should enhance the abundance of detritivores, because of the large quantities of plant litter produced by this invasive plant, and should enhance pollinator abundance due to its profusion of large and showy flowers.

Because some dune systems in California are almost entirely invaded by *Carpobrotus*, while others contain patches of native vegetation free of *Carpobrotus* adjacent to *Carpobrotus*-infested patches, I use two approaches to study its impacts. In the first approach I use paired invaded and uninvaded patches to evaluate differences in the arthropod assemblage. In the second approach I use plots in a gradient of *Carporbrotus* infestation including plots from a region where it is difficult to find uninvaded dune patches.

This study was designed to address the following questions:

1) Do arthropod abundance and richness, composition, and abundance of feeding guilds differ between paired plots with and without *Carpobrotus* across two sites? Here, I expected to find reduced overall arthropod abundance and richness in *Carpobrotus* versus native plots, and altered composition. I also predicted that the invasion would reduce the abundance of herbivores, predators, and parasitoids, but enhance the abundance of detritivores and pollinators.

2) How do the above arthropod response variables change along a gradient of increasing *Carpobrotus* cover both within and across three widely separated dune sites? I predicted a negative relationship between arthropod abundance/richness and *Carpobrotus* cover overall and for all feeding guilds except detritivores and pollinators. I had no a priori reason to expect differences in the shape of these relationships across the three sites.

Methods

Site descriptions

I identified three back dune sites along the Pacific coast in Ventura, Santa Barbara, and San Luis Obispo Counties, central California, which varied in levels of *Carpobrotus* cover and which contained similar native plant assemblages (Figure 1). Many *Carpobrotus* infestations in this region have been removed by land managers, with the densest *Carpobrotus* populations remaining on Vandenberg Air Force Base in Santa Barbara County. All sites share a Mediterranean climate moderated by coastal fog, with average maximum

temperatures (21-22° C) occurring in summer, average minimum temperatures (8-9° C) occurring in winter, and mean annual precipitation ranging from 37 to 42 cm/year (Western Regional Climate Center, Reno, NV: data from 1950 to 2005 at Lompoc/Vandenberg, 1900 to 2013 at Ventura, and 1959 to 1977 in Morro Bay/Montaña de Oro).

The Ventura County site, in the southeastern portion of San Buenaventura State Beach, is set within 1.8 km of continuous dunes, abutted by recreational and residential developments (35°16'11"N, 119°16'47"W). Dominant native plant species include *Ambrosia chamissonis*, *Abronia umbellata*, and *Camissonia cheiranthifolia.* Seven patches of *Carpobrotus* are found in the less developed, southern portion of the site whereas the remainder of the site has been cleared of *Carpobrotus*.

The Vandenberg Air Force Base site is located at southern Wall Beach just north of the Santa Ynez River among 5.7 km of continuous dunes, largely surrounded by undeveloped land (34°42'02"N, 120°36'03"W). Plant assemblages in these dunes are dominated by *Ambrosia chamissonis*, *Abronia maritima*, *Camissonia cheiranthifolia*, and *Ericameria ericoides*, with *Carpobrotus* distributed throughout.

The Montaña de Oro site is located in Montaña de Oro State Park, just north of the mouth of Hazard Canyon (35°18'17"N, 120°52'22"W), among 8.9 km of continuous dunes abutting primarily undeveloped land. Plant assemblages in the Montaña de Oro dunes are dominated by *Ambrosia chamissonis*, *Abronia maritima*, *Camissonia cheiranthifolia*, *Lupinus chamissonis*, and *Eriogonum parvifolium*. *Carpobrotus* is found in variably sized

patches scattered across the site.

Plot Selection: Paired plot analyses and gradient selection

At the Ventura and Montaña de Oro sites I selected discrete patches of *Carpobrotus* versus native dominated plots. At the Ventura site, one 6 X 6 m plot was established in each of seven *Carpobrotus* patches ≥ 40 square meters in area, and paired with similar sized plots in nearby areas dominated by native plant species. At Montaña de Oro I identified 12 areas with different levels of *Carpobrotus* cover, with each pair of areas generally separated by a ridge, trail, or distance of at least 15 meters. One *Carpobrotus* plot was haphazardly established within each of these areas, and adjacent paired native-dominated plots with similar slope and exposure were chosen.

Because *Carpobrotus* was more or less continuously distributed at the Vandenberg site, I selected and sampled eighteen random plots to represent a gradient of invasion, using DNR Random Sampling Tools (Minnesota Department of Natural Resources, St. Paul, MN) in Arcview 3.2 (ESRI, Redlands, CA), and a Trimble GeoXT Global Positioning System (GPS) unit (Trimble, Sunnyvale, CA). Where another invasive plant, *Ammophila arenaria*, was found in a selected plot, I moved the plot to the nearest location lacking this species.

Arthropod sampling was conducted in March and June of 2011 using both sand sifting and pan trapping techniques. For sand sifting, I took six 12 cm wide X 12 cm deep (1 liter) soil cores from a randomly chosen 2 x 2 meter subplot within each 6 x 6 meter plot, then sifted the collected soils through a 1mm mesh sieve, collecting organic material and

arthropods on both the sieve and a large shallow container placed below the sieve. The container and sieve were searched for a minimum of 3 minutes and any arthropods detected were aspirated and preserved in glass vials containing 70% ethanol. Even small mites were detected in this manner, as they moved across the sand. For pan trapping, I filled 18-cm diameter yellow plastic bowls with water and a few drop of dish detergent, then placed one bowl in the center of each plot and secured it with two wooden skewers. After three days and two nights, I collected the contents, sieved arthropods from the water, and transferred them to glass vials filled with 70% ethanol.

Vegetation Sampling

Vegetation was sampled in March 2011 using point-intercept transects. Four parallel six meter long transects, running northwest to southeast, were evenly spaced across each plot. Every half meter along each transect, I recorded the identity of each plant species intercepted, whether or not those species had flowers within one quarter meter on all sides of the point, the maximum height of plant interception, and substrate type (bare sand or plant litter). For each plot, these data were used to calculate percent *Carpobrotus*, native plant and litter cover; plant Shannon diversity (H'); *Carpobrotus* and non-*Carpobrotus* flower density (percent of all points with such flowers); and coefficient of variation for height (to assess structural diversity). In addition, plant litter was retained from sieve sampling, dried, and weighed to obtain litter biomass.

Arthropod Identification

All arthropods except mites (Acari) were identified to the family level; in addition, Coleoptera were identified to genus or species by an expert (Dr. Michael Caterino), Hymenoptera were sorted into "morphospecies" using morphological differences (Oliver & Beattie 1996), and Lepidoptera were identified to the finest taxonomic group possible by an expert (Dr. Jerry Powell). Mature Araneae were identified to species and immature Araneae were identified to family by an expert (Dr. Rick Vetter). In addition, ants and some Diptera were identified to the genus level when required for functional group determinations (see below). Most arthropod taxa were identified following Triplehorn and Johnson (2005), but identifications of Coleoptera followed Arnett and Thomas (2001) and Arnett et al. (2002), spiders followed Ubick et al. (2005), and isopods followed Smith and Carlton (1975). Mites could not be identified to family, so were used in the morphospecies diversity analysis but not the functional group analyses. Because there was less than one mite per plot, on average, this had little effect on the results. Voucher specimens are deposited at the Santa Barbara Museum of Natural History, Santa Barbara, CA.

Feeding Guilds

Each taxon (and different life stages of those taxa, when appropriate) was assigned to one of six feeding guilds (detritivore, herbivore, omnivore, pollinator, predator, and parasitoid) using Triplehorn & Johnson (2005) Arnett and Thomas (2001), Arnett et al. (2002), McAlpine et al. (1981), and McAlpine et al. (1987). For taxa known to have two

feeding habits within a given life stage, half of the individuals were included in the counts for each relevant feeding guild.

The detritivore group included all groups that use dead organic matter, including coprophages, fungivores, and scavengers. Nectarivores were divided into parasitoids and pollinators, because these two groups have different ecological and economic roles. Pollinators are important for crop production and are declining worldwide (Thomas et al. 2004, Winfree et al. 2009, Potts et al. 2010), while parasitoids are important for insect pest control (Price et al. 2011). Lastly, members of the family Cicadellidae (Hemiptera: Auchenorrhyncha) were analyzed both together and separately from other herbivore groups because they were the specialized herbivores most abundant in this study, and specialist herbivores are typically more negatively affected by exotic plant invasions than other herbivores (e.g., Novotny et al. 2003; Liu & Stiling 2006; Almeida-Neto et al. 2011).

Although ants were common, an ant nest was uncovered by soil samples in only one case with over one hundred individuals being present in that sample. In this case, ant abundance was adjusted downward to the next highest ant number found at that site. Only two feeding guilds were common in soil samples (detritivores and predators) and thus were the only two groups analyzed for this sampling technique.

Statistical Analyses

I used one-way ANOVAs and Tukey tests to compare vegetation attributes among treatments. Variables were log transformed (or log (x+1) transformed, when the data

contained zeros) when necessary to meet parametric test assumptions. I also used least-squares regression to examine relationships between *Carpobrotus* cover and both plant H' diversity and plant litter biomass (two variables hypothesized to drive feeding guild responses), using data from plots with *Carpobrotus* (all Vandenberg plots and *Carpobrotus* plots at the Ventura and Montaña de Oro sites).

I used paired t-tests where data met test assumptions, and Wilcoxon signed rank tests where they did not, to compare arthropod abundance and richness values between *Carpobrotus* plots and paired native plots at the Ventura and Montaña de Oro sites.

Both linear and polynomial regression analyses were performed using arthropod abundance and morphospecies richness as the dependent variables and *Carpobrotus* cover along with hypothesized habitat variables (plant H' diversity, plant litter biomass) as the independent variable. I used the Shapiro-Wilk test on raw variables and regression residuals to test for assumptions of normality, then used data transformations (primarily log (x + 1), to account for zeros in the data) when this assumption was not met. All of the above analyses were conducted in JMP 10.0 (SAS Institute, Cary, NC).

I used non-metric multidimensional scaling to visualize differences in the relative abundances of collected taxa across plots and treatments. In these analyses, I used family-level data rather than morphospecies data in order to include all arthropod taxa and to insure adequate numbers for analysis. I determined the effects of treatment on arthropod community composition using the Multi-response Permutation Procedure (MRPP) (Mielke and Berry 2001). Sorenson (Bray-Curtis) distance measures were used for both of these

analyses. In addition, Indicator Species Analysis was used to determine the families that were associated with specific treatments. All multivariate analyses were performed using PCOrd software, version 6 (McCune and Mefford 1999).

Results

I collected 6,605 arthropod individuals distributed among 20 orders and at least 139 families in soil and pan samples (Supplementary Information, Table S1). Within the Coleoptera and Hymenoptera, 239 species and morphospecies were identified, including 88 from Ventura, 105 from Vandenberg, and 158 from Montaña de Oro.

Vegetation characteristics, *Carpobrotus* vs. native plots

Vegetation characteristics in *Carpobrotus*-dominated plots vs. native plots analyzed by treatment and site are presented in Table 1. The following results are by plot type (*Carpobrotus* vs. native) for all three sites combined; note Vandenberg only had *Carpobrotus* plots. *Carpobrotus* plots had 73% lower native plant cover (CAED = 9.7 ± 2.0 SE; NTV = 35.6 ± 2.6 SE; $t = 6.1$, $p<0.0001$) and 63% lower plant H' diversity (CAED = 0.6 ± 0.08 SE; NTV = 1.6 ± 0.5 SE; $t = 7.0$, $p<0.0001$) than native plots. Plant diversity also decreased significantly with increasing *Carpobrotus* cover across the three sites (Figure 2). *Carpobrotus* plots had 37% lower plant species richness than native plots (CAED = 6.7 ± 0.6 SE; NTV = 10.6 ± 0.7 SE; $t = 3.7$, $p=0.0002$). Flower density was more than 2x greater in *Carpobrotus* plots than in native plots overall (CAED = 18.1 ± 3.1 SE; NTV = 8.1 ± 1.2 SE)

because of high *Carpobrotus* flower density (CAED = 16.4 ± 3.1 SE), but the overall difference was not significant (Wilcoxon test: Chi-square= 1.7, p=0.18). Coefficient of variation for height was 30% lower in *Carpobrotus* plots (CAED = 0.56 ± 0.04 SE; NTV = 0.80 ± 0.06 SE; t= 3.1, p=0.001). Plant litter biomass was nearly 4x greater in *Carpobrotus* plots (CAED = 30.9 ± 5.4 SE; NTV = 8.1 ± 1.6 SE; t= 3.5, p=0.001), than in native plots. Plant litter biomass also decreased significantly with increasing *Carpobrotus* cover at the three sites combined (Figure 3).

Arthropod responses: Paired analyses, *Carpobrotus* vs. native plots

Differences between paired *Carpobrotus* and native plots were not affected by site. Native plots tended to contain a greater abundance of arthropods than *Carpobrotus* plots across all samples (Fig. 5) with the strongest differences in March soil (p=0.07) and June pan traps (p=0.06). Native plots had significantly greater arthropod richness in all but June pan traps, however (Figure 5).

Detritivores were significantly more abundant in pan traps from *Carpobrotus* plots compared to native plots in both March and June (Figure 6A, B) but did not differ significantly in soil samples (Figure 7A). The lack of significance in this latter result is likely due to the small number of individuals captured; detritivores were more abundant in soil from native plots in both March and June.

Parasitoids and predators were significantly more abundant in native plots in March pan traps (Figure 6A), while omnivores showed a statistical trend in this direction (Figure

6A, p=0.08). In June, Cicadellidae (representing herbivore specialists), omnivores, parasitoids, and predators were all significantly more abundant in native plots (Figure 6B). Pollinators however, were significantly more abundant in *Carpobrotus* plots in June pan traps. Soil predators were significantly more abundant in native plots in March, but more abundant in *Carpobrotus* plots in June (Figure 7A, B).

Ordination results show significant compositional differences between paired *Carpobrotus*/native plots in June pan traps (Figure 8). Empidiidae (predators) and Melyridae (omnivores) were indicator species for native plots in June, while Heleomyzidae (detritivores) and Halictidae (pollinators) were characteristic of *Carpobrotus* plots. There was no significant difference in arthropod composition between *Carpobrotus* and native plots in March pan traps (MRPP: t= -0.60, A = 0.004, p= 0.24). No useful ordination solution was found for soil samples, even when the two sample months were combined, due to low abundances in each family.

Arthropod responses to increasing *Carpobrotus* cover: General findings

Arthropod responses to *Carpobrotus* often differed by site (Supplementary Information, Table S2). For example, pan-trapped arthropod abundance increased significantly with *Carpobrotus* cover at Ventura and Vandenberg Air Force Base in June (Figure 9A), but no relationship was found at Montaña de Oro. Soil arthropod abundance increased marginally with increasing *Carpobrotus* cover at Montaña de Oro in June (Figure 9B), but not at the other two sites. In contrast, arthropod abundance decreased with

Carpobrotus cover in March pan traps at Vandenberg Air Force Base (Figure 9C), but no significant relationships were found at the two other sites.

Arthropod richness was generally not correlated with *Carpobrotus* cover except for two cases: (1) A significant negative relationship was found at all sites in June pan traps (Rich = 31.31 - 3.36 * log (CAED + 1); Rsquare 0.17; β = -3.36, t = -2.70; p=0.01), and (2) A significant positive relationship was found between *Carpobrotus* cover and June soil arthropods at Montaña de Oro (Log (Rich + 1) = -0.65 + 0.53 * log (CAED + 1); Rsquare = 0.41; t=2.64, p=0.03).

Functional group responses to *Carpobrotus* cover

Both soil detritivores and pan-trapped detritivores decreased significantly with increasing *Carpobrotus* cover at Vandenberg in March (Figures 10A, 11A); no other significant relationships were found for *Carpobrotus* cover versus detritivores. At Montaña de Oro, a significant negative relationship was found between soil detritivores and litter biomass in March (Log (Detr + 1) = 1.56 - 0.34*log (LitBio + 1); Rsquare = 0.37, t= -2.43, p=0.04), but a positive trend was found in June (Log (Detr + 1) = -0.70 + 0.42 log (litbiom + 1); Rsquare = 0.30, t=2.08, p=0.06). A positive relationship to litter biomass was also found in June at Ventura (Log (Detr + 1) = 0.67 + 0.44*log (LitBiom + 1); Rsquare 0.68). t=3.25, p=0.02). No significant relationship was found between pan trapped detritivores and litter biomass in either month at Vandenberg.

Soil predators had a significant positive relationship with *Carpobrotus* cover in June

at Montaña de Oro and Vandenberg (Figure 10B), but no significant relationship for any site in March or Ventura in either month. Similarly, soil predators exhibited a significant negative relationship with plant H' diversity in June at Montaña de Oro (Log (Pred + 1) = 1.61 - 1.41 *PlntDiv; Rsquare = 0.58, t= -3.7, p=0.004). In contrast, soil predators exhibited a significant positive relationship with plant H' diversity at Vandenberg in March (Log (Pred + 1) = 0.29 + 0.64 *PlntDiv; Rsquare 0.21, = 2.06, p=0.06).

Pan-trapped predators decreased with increasing *Carpobrotus* cover in March at Ventura and in June at all sites (Figures 11F, 12F). Similarly, pan trapped predators increased significantly with plant H' diversity at all sites in June (Log (Pred + 1) = 1.35 + 0.70 *H'; Rsquare 0.19, t=2.90, p=0.006), but no significant relationships were found in March pan traps.

Herbivores decreased with increasing *Carpobrotus* cover in March pan traps at Ventura (Figure 11B), and showed a significant positive relationship with plant H' diversity (Log (Herb + 1) = 0.51 + 1.62*H'; Rsquare= 0.80, t=4.54, p=0.006). In contrast, herbivores increased in June pan traps at Vandenberg (Figure 12A), and had a negative relationship with plant H' diversity (log (Herb + 1) = 4.57 - 1.19 *H'; Rsquare =0.29, t= -2.56, p=0.02).

When only specialist herbivores in the family Cicadellidae were considered, the results were similar: a decrease with *Carpobrotus* cover in March at Ventura (Log (Cicadl + 1) = 7.36- 1.52 *log (CAED + 1); Rsquare = 0.68, t= -3.3, p=0.02) and an increase in June at Vandenberg (Figure 12B). The only significant relationship found between Cicadellidae and plant H' diversity was at Ventura in March, and it was positive (Log (Cicadl + 1) = 0.08 + 1.64

* H'; Rsquare= 0.91, t=7.14, p=0.0008).

Omnivores decreased at all sites in June (Figure 12C). Similarly, a positive relationship with plant H' diversity was consistent across all sites in June (Log (Omn + 1) = 1.06 + 0.82*H'; Rsquare =0.15, t=2.47, p=0.02). Omnivores could not be analyzed in March due to very low numbers.

Parasitoids decreased with increasing *Carpobrotus* cover in March pan traps at Ventura (Figure 11C), in accordance with predictions. Similarly, March parasitoids increased with plant H' diversity at Ventura (Log (Para + 1) = 0.39 + 0.55 *H'; Rsquare= 0.76, t=3.94, p=0.01) and at Montaña de Oro (Log (Para + 1) = 1.03 + 0.78 *H'; Rsquare 0.34, t=2.27, p=0.05). Parasitoids also trended toward a positive relationship with plant H' diversity at Vandenberg in June (Log (Para + 1) = 1.06 + 0.59 *H'; Rsquare 0.19, t=1.96, p=0.07).

While pollinators decreased at Vandenberg with increasing *Carpobrotus* cover (significantly in June, and marginally in March), they increased at Ventura in both months; this increase was exponential at Ventura in March, but marginal in June (Figures 11D, 11E, 12D, 12E). Similarly, June pollinators at Vandenberg increased with plant H' diversity (Log (Poll + 1) = 0.53 + 1.49*H'; Rsquare 0.42, t=3.38, p=0.004) and March pollinators at Ventura decreased with plant H' diversity (Log (Poll + 1) = 2.41 - 1.18 * PlntDiv; Rsquare 0.67, t= -3.20, p=0.02).

Ordination revealed significant compositional differences in *Carpobrotus* plots between all three sites in both March (Figure S1) and June (Figure S2). In March pan traps,

a significant difference was found in arthropod composition between plots with 30% or less cover and all other cover classes (Figure 13). Chloropidae were indicative of native-dominated plots, while Andrenidae and Isotomidae were associated with plots having 90% or more *Carpobrotus* cover. A gradual change in composition was found in June (Figure 14), from plots with 0-30% *Carpobrotus* cover to those with 30-50%, 50-70%, 70-90%, and >90% cover. Melyridae, Braconidae, and Chloropidae were particularly indicative of native-dominated plots, while Entomobryidae was common in *Carpobrotus*-dominated plots.

Although ordination analyses could not be performed on soil data, one taxon was obviously negatively impacted by *Carpobrotus* invasion: the ciliate dune beetle, *Coelus ciliatus* (Tenebrionidae). Immature *Coelus* had a significant negative exponential relationship with *Carpobrotus* cover in March (Polynomial regression: #*Coelus* = 1.54 - 0.03 * %CAED + 0.0005 * (%CAED-48)^2; Rsquare = 0.26. %CAED: t= -3.44, p=0.002; (%CAED - 48)^2: t= 1.88, p=0.07).

Discussion

General patterns:

The relationships between arthropod variables and *Carpobrotus*/native plant variables depended on site, strata/sampling type (soil versus pan traps) and *Carpobrotus* cover. Where it was possible to compare arthropod assemblages in paired native/non-native dominated plant plots (Montaña de Oro and Ventura), I found that as predicted,

there was a significant negative effect of *Carpobrotus* on overall arthropod *richness* in three out of four season/method combinations. Effects of *Carpobrotus* on arthropod *abundance* in these same samples were weaker than predicted but evident in two of the four combinations, where abundance was higher in native plots than *Carpobrotus* plots. Ordination analyses also revealed differences in arthropod composition by plot type, as predicted, as well as by site. Specifically I found significant compositional differences between pan trapped arthropods from *Carpobrotus* versus native plots in June (but not March).

In contrast to the paired difference values discussed above, and contrary to predictions, arthropod responses to increasing *Carpobrotus* cover (regression approach) often differed in sign and strength at the three sites and overall few significant relationships were found. Sometimes, significant patterns were opposite in different seasons; for example, at Vandenberg Air Force Base arthropod abundance decreased with *Carpobrotus* cover in March, but increased in June. These trends were related to those of feeding guilds such as detritivores, which decreased in March, and herbivores, which increased in June. In addition, arthropod composition was significantly different between all sites in both seasons, suggesting that the different taxonomic groups at different sites are important influences on the responses to *Carpobrotus* invasion. Importantly, a strong shift in arthropod composition was evident at a *Carpobrotus* cover threshold of 30% in March (Figure 13), while a more gradual but significant change in composition was found in June (Figure 14).

As with paired analyses, richness results were generally stronger than abundance results for regression analyses. A significant negative relationship was found between *Carpobrotus* cover and arthropod richness at all sites in June pan traps, for example. However, soil arthropod richness increased with *Carpobrotus* cover at Montaña de Oro in June, and other sites/seasons did not show significant relationships. The positive response by soil arthropods appears to have been driven by predators, which are discussed below along with other feeding guilds.

Functional groups:

Consistent with my predications, omnivores, parasitoids, and pan-trapped predators were all consistently more abundant in uninvaded plots. Contrary to predictions, both soil and pan-trapped detritivores sometimes decreased with increasing *Carpobrotus*, soil predators sometimes increased with *Carpobrotus*, and both herbivores (including just specialist herbivores in the family Cicadellidae) and pollinators exhibited both negative and positive relationships with *Carpobrotus* cover at different sites and times. In addition, many relationships were not significant. Below I discuss those relationships that appeared to be most consistent or dramatic.

Invasive plants often produce high plant litter levels over successive growth cycles (Hartley et al. 2004; Gratton and Denno 2005; Kappes et al. 2007; Topp et al. 2008; Holdredge and Bertness 2011), and *Carpobrotus* is no exception; plant litter biomass was nearly 4x greater in *Carpobrotus* plots (and see Molinari et al. 2007). Yet across all

Carpobrotus plots, pan-trapped detritivores had a significant negative relationship with *Carpobrotus* at Vandenberg in March, and no other significant relationships were found with either *Carpobrotus* or litter biomass. Soil detritivores were not significantly different between native and *Carpobrotus* plots, but as with pan-trapped detritivores, decreased with increasing *Carpobrotus* cover at Vandenberg in March. It is possible that *Carpobrotus* litter accumulates because chemically it is relatively resistant to decay and thus detritivore populations do not build up to high levels in its litter. Numerous studies have demonstrated rapid decomposition of alien plant litter (reviewed by Liao et al. 2008) but none of the reviewed species include salt-concentrating Aizoaceae (Vivrette and Muller 1977) such as *Carpobrotus*. We did find that some detritivores (such as flies in the family Chloropidae and dune beetles in the family Tenebrionidae) preferred the more native plots, while some (such as springtails in the families Entomobryidae and Isotomidae, and barklice in the family Psocidae) preferred plots where *Carpobrotus* dominated. By contrast, Wolkovitch et al. (2009) found that the same two families of springtails were less abundant in areas of high invasive annual grass density in otherwise native California shrublands. While it has been suggested the detritivorous taxa are relative generalists (Srivastava et al. 2009), a literature review has shown that few studies show a positive response by detritivores to plant invasions (Chapter 1). Thus detritivores may be more specialized than previously thought and few taxa may be able to utilize *Carpobrotus* litter.

It may also be the case that the detritivore response was tempered by the effects of *Carpobrotus* on habitat structure or disturbance regime (Ribeiro-Troian et al. 2009;

Wolkovitch et al. 2009). In this study the abundance of the common, detritivorous dune beetle, *Coelus ciliatus*, was negatively related to *Carpobrotus* cover, declining to zero at around 60% *Carpobrotus* cover. I suggest that the negative effects of *Carpobrotus* on the abundance of this fossorial insect are driven by less diverse plant food resources in *Carpobrotus* areas and by dense *Carpobrotus* roots (D'Antonio and Mahall 1991) which could readily inhibit insect movement.

Omnivores, dominated by soft-winged flower beetles (Melyridae: Dasytinae), showed one of the strongest negative responses to *Carpobrotus* invasion, and a positive relationship with plant H' diversity. Dasytine melyrids frequent flowers and often feed on nectar and pollen (Mawdsley 2003), so these results may represent a preference for native over *Carpobrotus* flowers, perhaps due to chemical or nutritional differences. Melyrids can also be classed as pollinators (Mawdsley 2003).

Herbivores did not exhibit a significant difference between native and *Carpobrotus* plots in either month, and in *Carpobrotus* plots had both negative and positive relationships with *Carpobrotus* cover in different sites and months. Herbivore relationships with plant H' diversity also varied, and were the opposite of *Carpobrotus* effects. I expected specialist herbivores to respond more negatively to *Carpobrotus* invasion, as most studies find that alien plants host a greater proportion of generalist than specialist herbivore species (Chapter 1). However, while specialists (Cicadellidae) were more abundant in native plots in March, they favored *Carpobrotus* plots in June, and showed similar patterns to herbivores as a whole. Although insect herbivores, particularly specialists, may not use a

novel plant species because of differences in characteristics such as nutritional quality, chemical composition, and architecture (Strong et al. 1984; Haynes and Kronin 2003; Novotny et al. 2003; Liu & Stiling 2006; Kuhnle and Muller 2009; Carvalheiro et al. 2010), more taxa typically colonize over time (Strong et al. 1984; Harvey et al. 2013). Since *Carpobrotus* has been on the central coast of California for over 100 years, it seems that several herbivores, such as members of the Cercopidae and Cicadellidae, have successfully colonized it. Further, herbivores are likely responding to the abundance of their host plants, as *Carpobrotus* reached its highest abundance at Vandenberg, where herbivores increased, and lowest abundance at Ventura, where herbivores decreased with *Carpobrotus* cover.

Pollinators were significantly more abundant in *Carpobrotus* plots in June (but did not differ in March), and, contrary to predictions, showed contrasting responses to increasing *Carpobrotus* cover, decreasing at one site (Vandenberg) but increasing at another (Ventura) in both months (with the opposite relationship to H' plant diversity). This discrepancy may be due to the different landscape-scale abundance of *Carpobrotus* at these two sites. At Vandenberg, *Carpobrotus* is abundant throughout the landscape, and thus likely depressing overall plant diversity (given the negative relationship between *Carpobrotus* cover and plant H' diversity shown in Figure 2). At Ventura, however, it is found only in small patches which are likely not yet depressing landscape-level plant diversity, but rather attracting pollinators via its large, abundant, and showy flowers. Moragues and Traveset (2005) demonstrated the high attractiveness of *Carpobrotus*

species to pollinators in the Mediterranean basin, where members of the genus are also invasive. Indeed, alien plants have been shown to attract pollinators in several cases, with potentially both competitive and facilitative effects for co-occurring native plant species (Traveset and Richardson 2006, Bjerknes et al. 2007). Those pollinators are typically less diverse, however (Chapter 1), which is likely due to a decline in specialist taxa (Biesmeijer et al. 2006). Indeed, most pollinators at my sites were bees in the genera *Lasioglossum* and *Agapostemon* (Halictidae), *Ceratina* (Apidae), *Bombus* (Apidae), and *Apis* (Apidae), which are primarily generalists (Anderson 1984; Dr. Robbin Thorp, pers. comm.).

Parasitoids were consistently less abundant in *Carpobrotus* plots than native plots, as predicted. This pattern could potentially be explained by a decrease in the availability of their prey (Petermann et al. 2010; Scherber et al. 2010), as gross feeding guilds were more abundant in native plots in nearly all cases. This cannot be determined definitively, however. In addition, foraging efficiency and predator avoidance are reduced in structurally simplified vegetation (Langellotto & Denno 2004), and the invaded areas had 30% lower variation in vegetation height. Structurally complex habitats (those with greater plant heights, species, or detritus) not only provide a refuge but also supplementary food such as nectar, pollen, fungi, and plant fluids (Brose 2003; Langelotto & Denno 2004; Price et al. 2011). Despite the strong differences in paired plots, however, parasitoids only showed a significant (negative) relationship with *Carpobrotus* cover in one of six site/season combinations (Ventura in March). This follows from the few significant relationships found in other feeding guilds, and may indicate that effects are already great

at low levels of invasion, and only revealed through a paired plot approach.

Pan-trapped predators preferred native plots to *Carpobrotus* plots in both months, decreased in the majority of site/season combinations with increasing *Carpobrotus* cover, and increased with plant H' diversity at all sites in June. Soil predators, on the other hand, were more variable, favoring native plots in March and *Carpobrotus* plots in June, and were positively related to *Carpobrotus* cover in June at two of three sites. As with parasitoids, these patterns could potentially be explained by a decrease in the availability of their prey.

Clearly, composition differences were important in the varying results seen here between seasons and sites. In some instances, one taxon or feeding guild may be responding positively to invasion (such as above-ground detritivores including Entomobryidae in this study), while others (such as Melyridae and parasitoids) may be responding negatively, potentially masking important ecological effects when only overall abundance or richness are considered. The fact that there was no significant compositional difference between native and *Carpobrotus* paired plots in March pan traps may be one of the reasons that there were fewer significant differences between paired plots in that month; lower arthropod abundance overall (~1/3 that of June) may also have contributed. Further, both compositional differences and landscape-scale differences in *Carpobrotus* cover are likely influencing the site differences seen in this study.

<u>Assessing species impacts:</u>

Numerous studies have attempted to assess the impacts of a non-native plant on

arthropod abundance, with varying results (e.g., Loomis and Cameron 2014; Emery and Doran 2013). In addition to the intrinsic variability and high complexity of arthropod assemblages, variation among studies may be the result of sample design. Here I found that results were generally stronger using a paired plot approach (Montaña de Oro and Ventura) with *Carpobrotus* presence/absence as a discrete categorical factor. The regression approach, which treats individual plots as points across all values of cover of the invader, gave more equivocal results. I believe this is because strong impacts are occurring with any degree of *Carpobrotus* invasion. This hypothesis is supported by the finding of a strong difference in composition at 30% cover. It is also supported by results at another site, Coal Oil Point (Chapter 3). Similarly, in a theoretical treatment of invader impacts, Aizen et al. (2008) demonstrate that invasive plant impacts increase disproportionately to their abundance due to functional effects on associated organisms. Hence although it is appealing to sample an invader across varying levels of invasion, a combination of analyses including evaluation of compositional shifts is likely to yield the most insight into how invader impacts arise.

Conclusion

While numerous studies have evaluated the effect of particular plant invaders on arthropod assemblages, most have focused narrowly on a particular group or have sampled at only one site. By sampling over multiple sites, two time points and using more than one arthropod sampling method, my study provides valuable insight into the complex

ways that a single plant species can alter the composition of a diverse invertebrate assemblage. Despite variation driven by the timing and method of sampling, I found that overall, *Carpobrotus edulis* invasion is significantly altering arthropod assemblages in the coastal dunes of California. The most significant of these effects can be seen between paired invaded and uninvaded plots, where richness and abundance are typically reduced, and arthropod community composition is altered. Omnivores, parasitoids, and predators responded most negatively to *Carpobrotus* invasion, while aerial detritivores responded mostly positively and pollinators had different responses at different sites. More important than feeding guild, however, appears to be responses by the individual taxa themselves. These findings have negative implications for wildlife that prey on arthropods, including birds, herpetofauna, and small mammals, as well as the ecosystem functions that they are performing (van Riper et al. 2008; Gullan and Cranston 2005).

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Table 1. Vegetation characteristics at Montaña de Oro (MDO), Vandenberg Air Force Base (VAN), and San Buenaventura State Beach (VEN) in plots with *Carpobrotus* vs. those that are native-dominated.

	Treatment/Site				
	***Carpobrotus*: MDO**	***Carpobrotus*: VAN**	***Carpobrotus*: VEN**	**Native: MDO**	**Native: VEN**
n	12	18	7	12	7
% *Carpobrotus* cover	55	38	60	7.8	0
	(7.4)	(5.6)	(12.2)	(1.5)	(0)
	A	A	A	B	C
% Native cover	3.4	12.2	12.1	34.7	37.3
	(1.5)	(3.1)	(5.5)	(3.2)	(4.7)
	A	A	A	B	B
Plant H' diversity	0.40	0.65	0.80	1.6	1.5
	(0.13)	(0.09)	(0.28)	(0.06)	(0.07)
	A	A	A	B	B
Plant species richness	6.0	5.9	9.7	12.0	8.1
	(1.4)	(0.6)	(1.5)	(0.9)	(0.6)
	A	A	AB	B	AB
Carpobrotus flower density (% of all points)	20.7	13.1	19.0	0	0
	(4.7)	(4.6)	(8.9)	(0)	(0)
Non-Carpobrotus flower density (% of all points)	0.9	1.9	2.4	6.6	10.7
	(0.5)	(1.2)	(1.3)	(1.3)	(1.9)
Coefficient of height variation	0.54	0.59	0.52	0.78	0.84
	(0.08)	(0.06)	(0.04)	(0.08)	(0.07)
	A	A	A	A	A
Litter biomass (g/L)	44.7	20.0	33.9	11.9	1.6
	(10.9)	(4.6)	(15.9)	(1.8)	(0.3)
	A	A	A	A	B

Note: n is the number of plots in each category; numbers in the body of the table are mean values and numbers in parentheses are SEs for means. Capital letters below this indicate statistically significant differences between sites within a treatment based on ANOVA and Tukey tests. All variables were log (or log (x + 1)) transformed to meet test assumptions. VAN= Vandenberg, VEN = Ventura, and MDO = Montaña de Oro. Flower density could not be assessed with ANOVA due to non-normality of right-skewed data, even when log transformed.

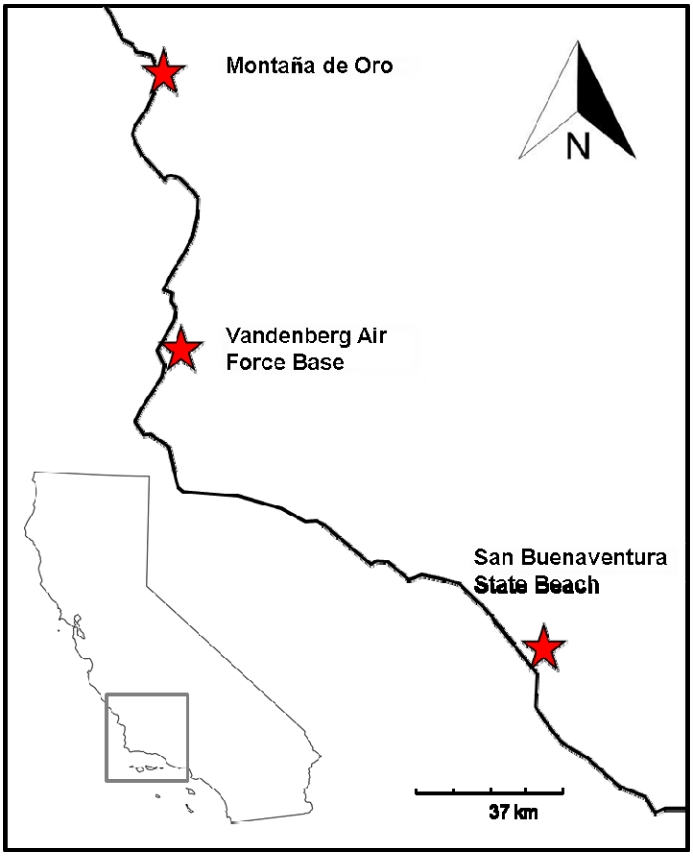


Figure 1. Three sites sampled for plants and invertebrates along the central coast of California (indicated by stars). Montaña de Oro is located at 35°18’17”N, 120°52’22”W, Vandenberg Air Force Base is located at 34°42’02”N, 120°36’03”W, and San Buenaventura is located at 35°16’11”N, 119°16’47”W.

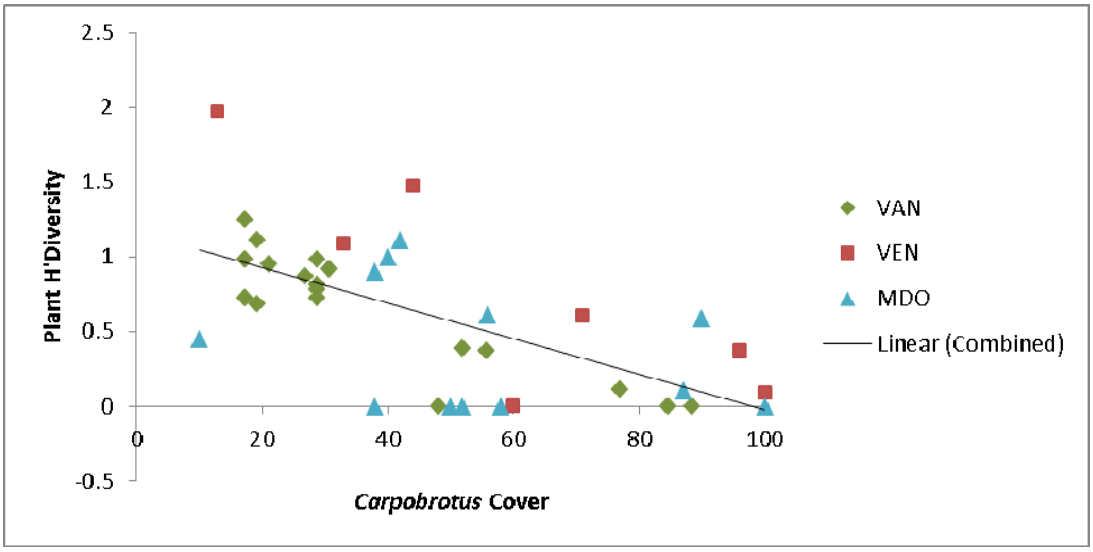


Figure 2. Relationship between % *Carpobrotus* cover and plant H' diversity at all sites (which were not significantly different). Variables were log (x+1) transformed for analysis to meet test assumptions. Least squares regression equation = Log (Plant H' + 1) = 1.65 - 0.33*Log CAED. Rsquare = 0.43, t=-5.14, and p<0.0001.

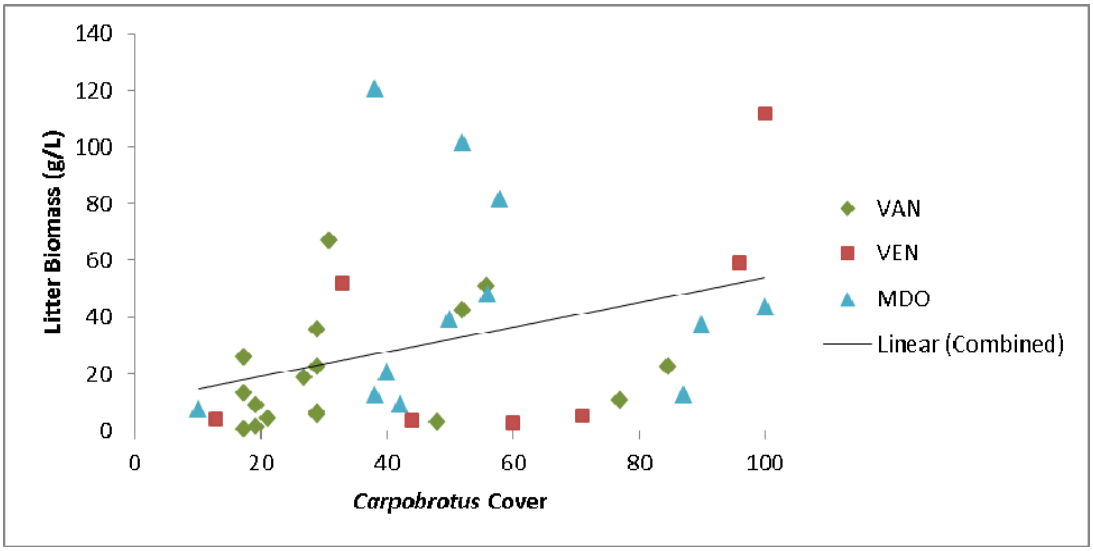


Figure 3. Relationship between *Carpobrotus* % cover and litter biomass at all sites (which were not significantly different). Variables were log (x+1) transformed for analysis to meet test assumptions. Least squares regression equation = log (LitBiom + 1) = -0.28 + 0.86*log (CAED + 1). Rsquare = 0.20, t=-2.89, and p=0.007.

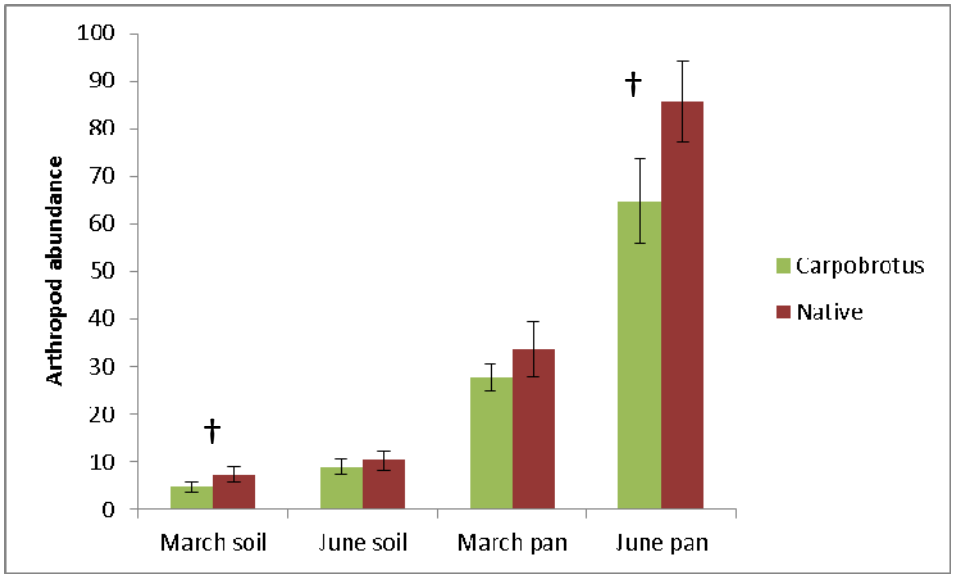


Figure 4. Mean soil arthropod abundance (± 1 SE) in *Carpobrotus* and paired native plots at the Ventura and Montana de Oro sites. The symbol † indicates significance at the $0.05 \leq p \leq 0.1$ level (paired t-tests).

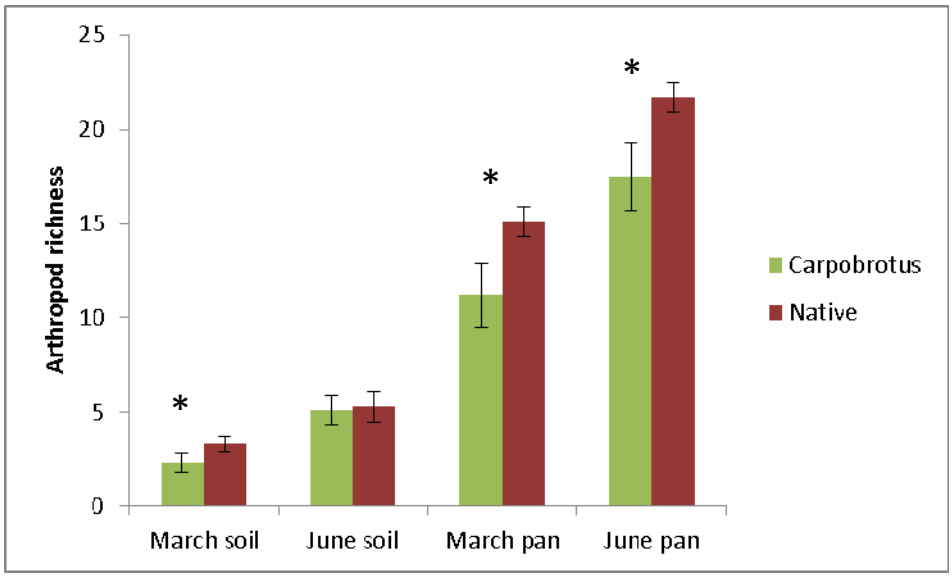


Figure 5. Mean arthropod richness (± 1 SE) in *Carpobrotus* and paired native plots at the Ventura and Montaña de Oro sites. The symbol * indicates significance at the $0.01 \leq p \leq 0.05$ level (paired t-tests).

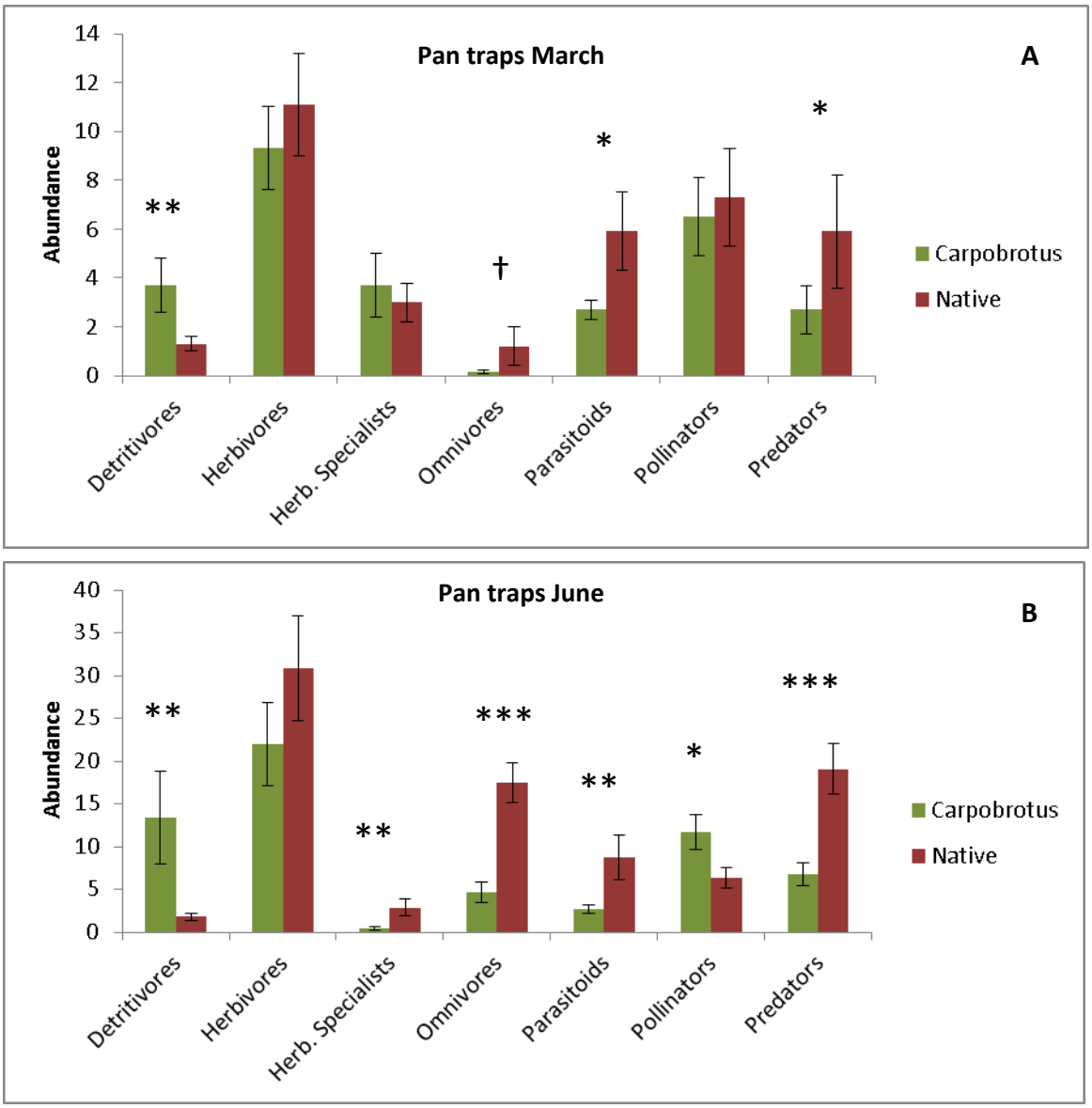


Figure 6. Average abundance of arthropod feeding guilds (± 1 SE) in *Carpobrotus* and paired native plots at the Ventura and Montana de Oro sites in March (top) and June (bottom) pan traps. Symbols indicate significance: * $0.05 > p \geq 0.01$, ** $0.01 > p \geq 0.001$, *** $p < 0.001$ (paired t-tests).

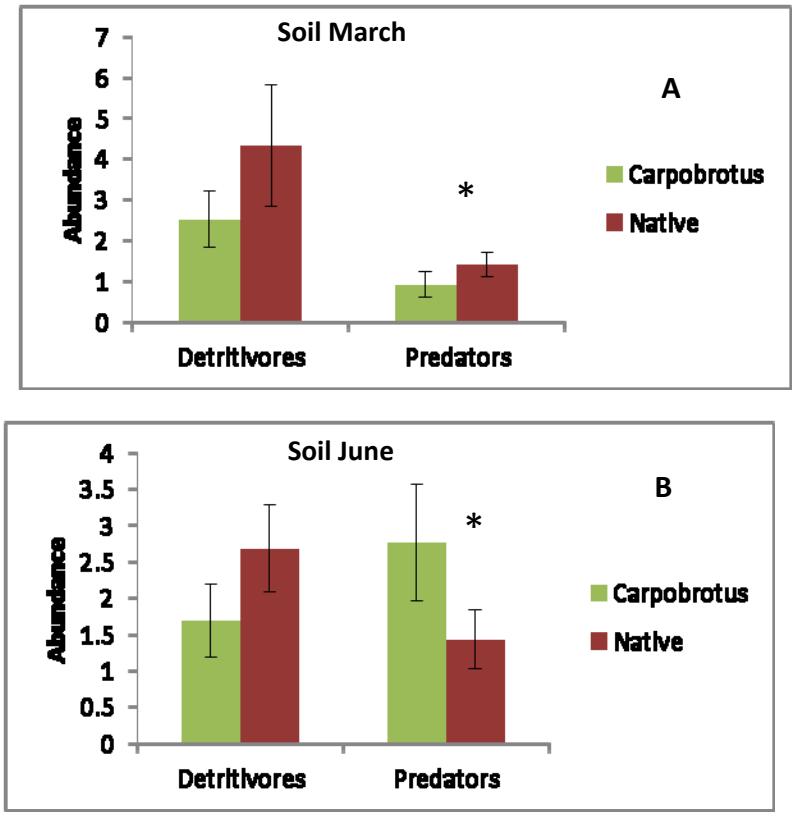


Figure 7. Average abundance of arthropod feeding guilds (± 1 SE) in *Carpobrotus* and paired native plots at the Ventura and Montana de Oro sites in March soil (top) and June soil (bottom). The symbol * indicates significance at the $0.01 \leq p \leq 0.05$ level (paired t-tests for predators in June, signed-rank tests for rest).

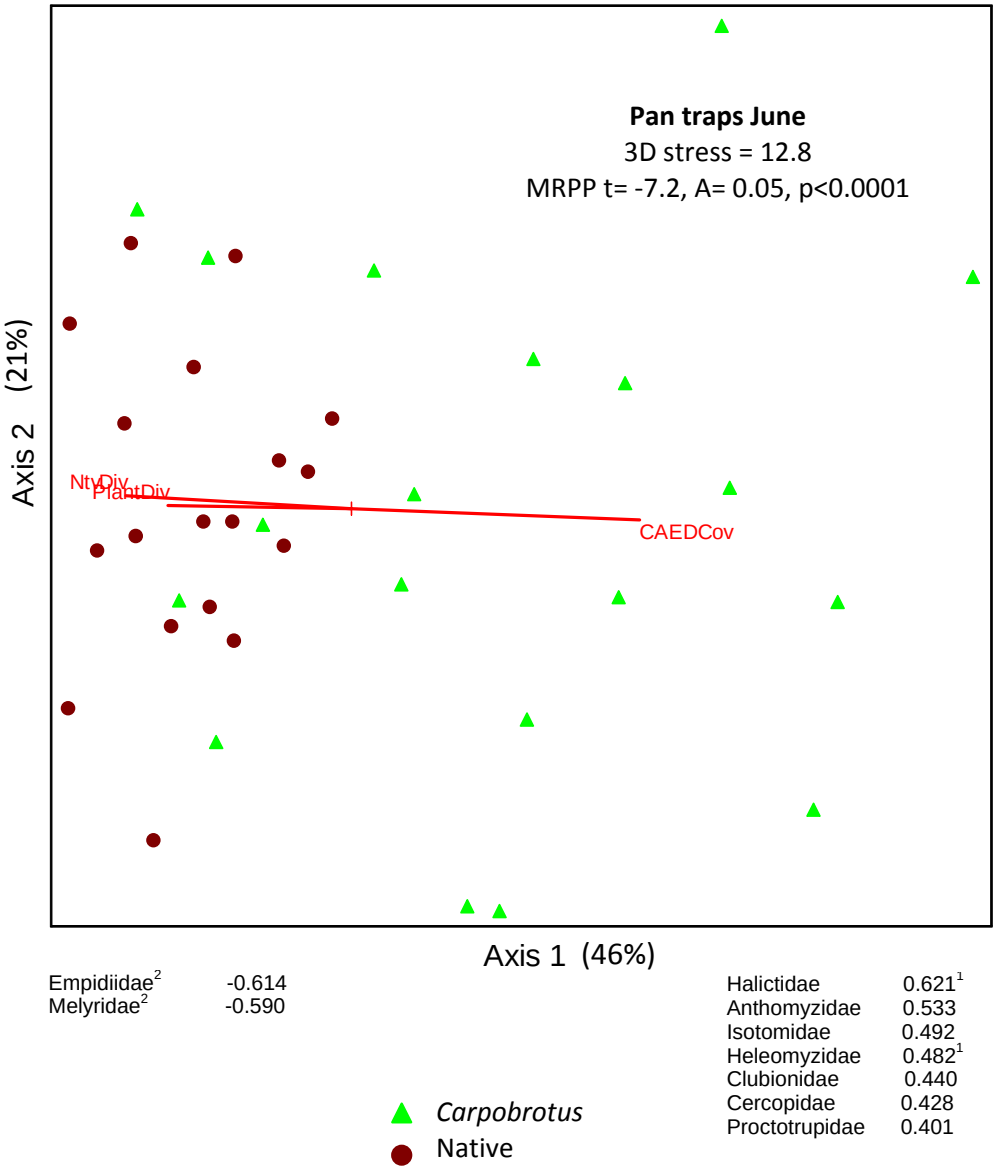


Figure 8. Results of a nonmetric multidimensional scaling (NMDS) analysis applied to the matrix of the relative abundances of all arthropod families in June pan traps, by plot type (native, *Carpobrotus*) at all sites. Families correlated with the axis most relevant to *Carpobrotus* cover classes (Axis 1) and their Pearson's correlation coefficients are noted in the margins of the diagram; superscripts denote indicator species for *Carpobrotus*[1] or Native [2] plots. Vectors indicate the vegetation variables most associated with the axes: *Carpobrotus edulis* (CAED) cover, plant H' diversity, and native plant H' diversity. Numbers in parentheses indicate the percent variation accounted for by each axis.

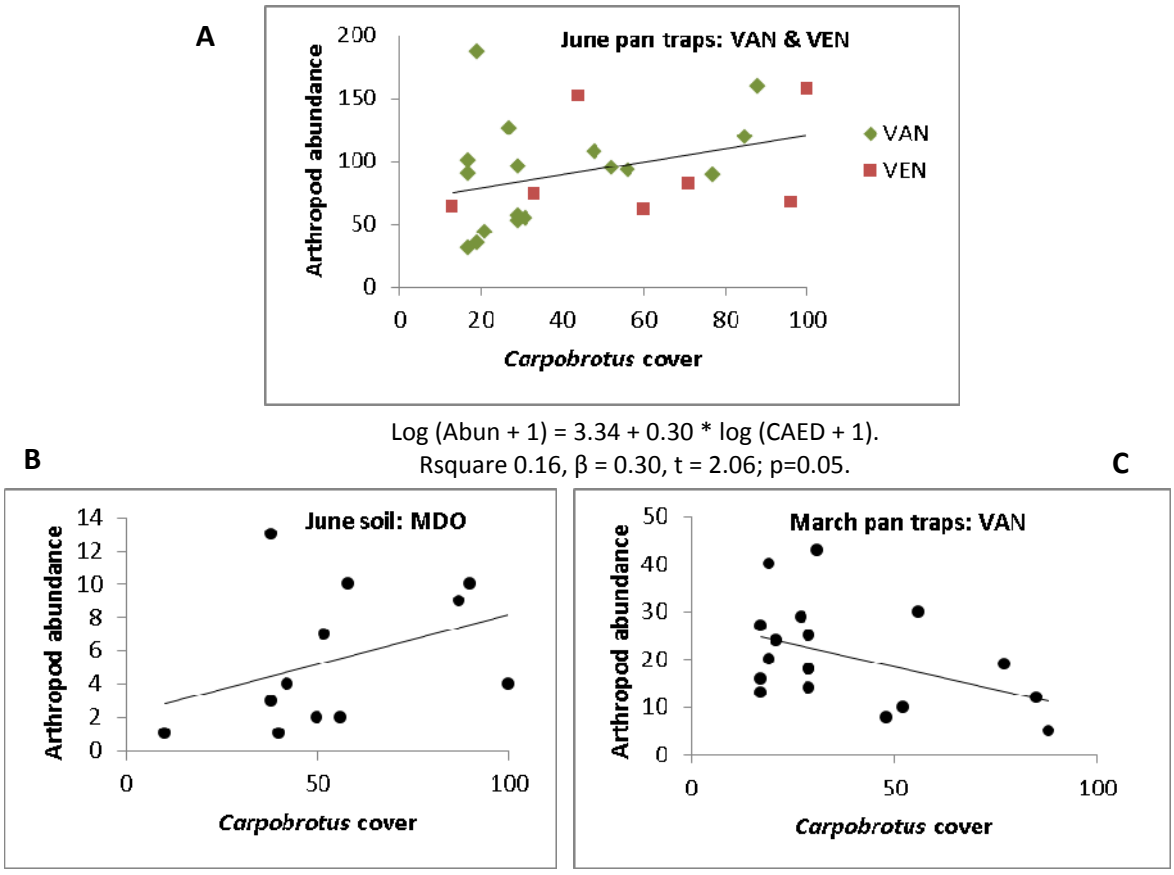
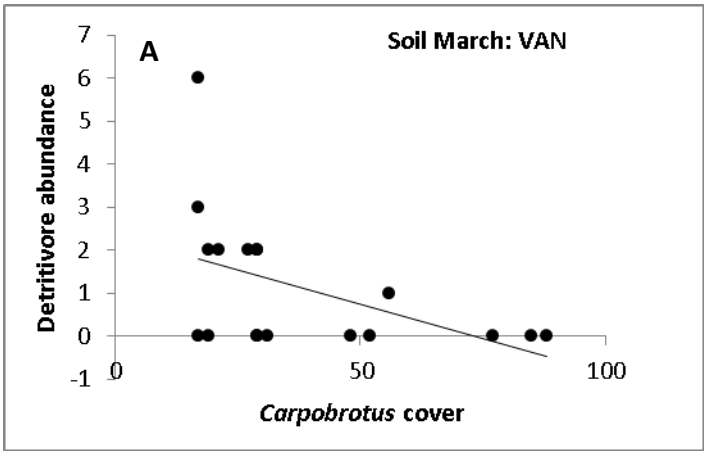
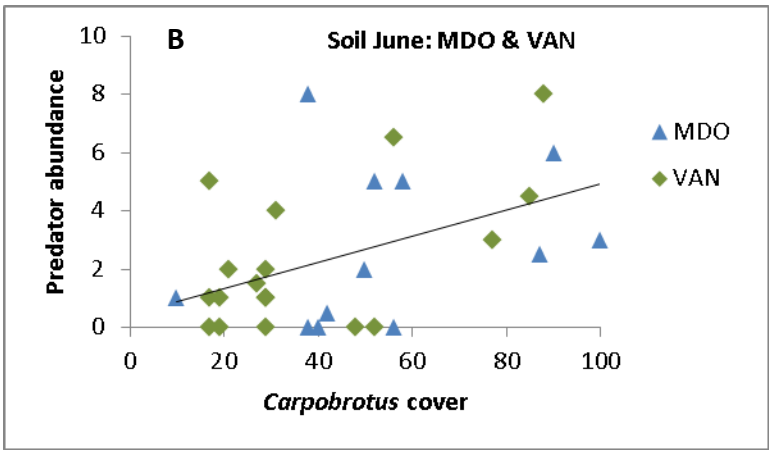


Figure 9. Significant relationships between *Carpobrotus* cover and arthropod abundance. MDO = Montaña de Oro, VAN = Vandenberg Air Force Base, and VEN = San Buenaventura State Beach.

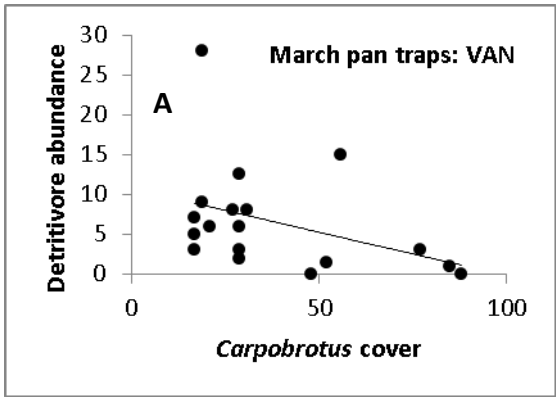


Log (Detr + 1) = 2.76 - 0.63*Log (CAED + 1);
Rsquare = 0.29, t= -2.53; p=0.02.

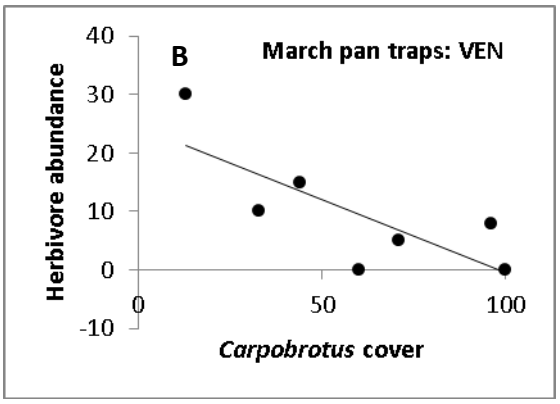


Log (Pred + 1) = -0.91 + 0.51*log (CAED + 1).
Rsquare = 0.15, t=2.26; p=0.03.

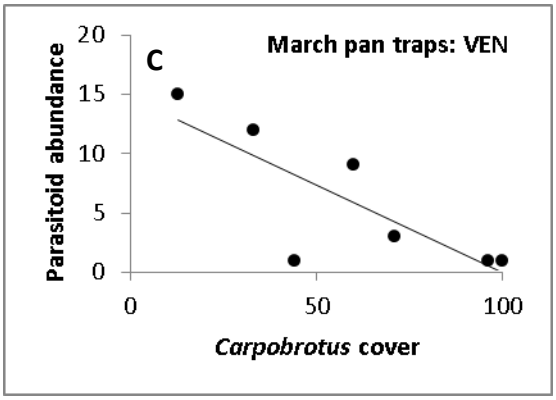
Figure 10. Significant relationships between *Carpobrotus* cover and functional group abundance in soil. MDO = Montaña de Oro, VAN = Vandenberg Air Force Base, and VEN = San Buenaventura State Beach.



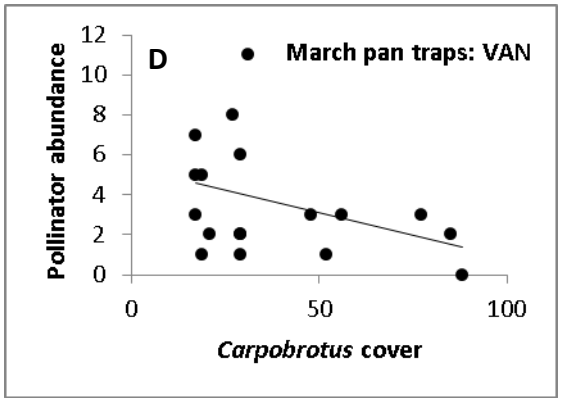
Log (Detr + 1) = 4.97 - 0.94*log (CAED + 1); Rsquare 0.32, t= -2.77, p=0.01.



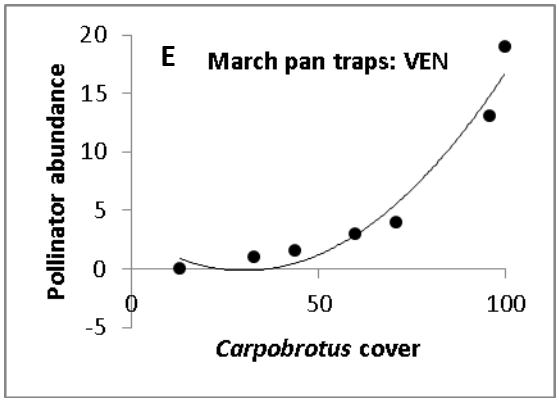
Log (Herb + 1) = 6.96 - 1.31*log (CAED + 1); Rsquare = 0.47, t= -2.09, p=0.09.



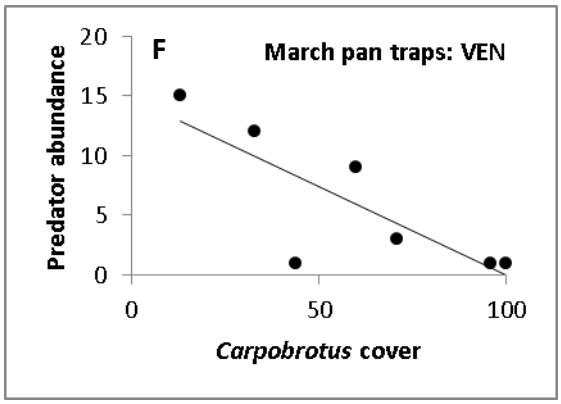
Log (Para + 1) = 3.03 - 0.56*log (CAED + 1); (Rsquare = 0.69, t= -3.31, p=0.02).



Log (Poll + 1) = 3.04 - 0.48*log (CAED + 1): Rsquare = 0.18, β= -0.48, t = -1.86, p=0.08.

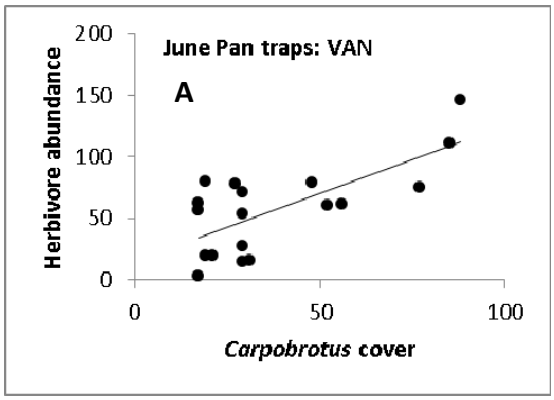


Polynomial fit: -9.30 + 0.20* CAEDcov + 0.003*(CAEDcov-59.57)^2; Rsquare 0.95, t = 8.51 for CAEDcov, p=0.001; t = 3.79, p=0.02 for CAEDcov-60.

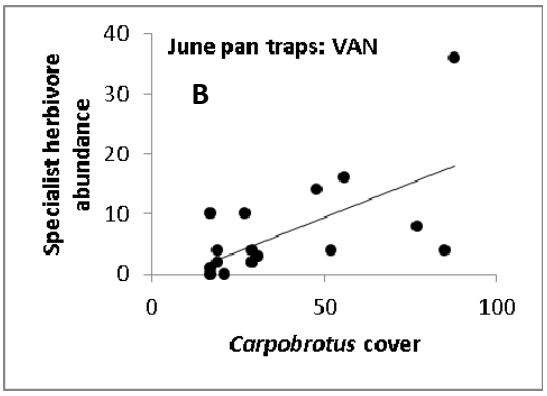


Log (Pred + 1) = 5.61 - 1.02*log (CAED + 1); Rsquare = 0.57, β = -1.02, t= -2.55, p=0.05.

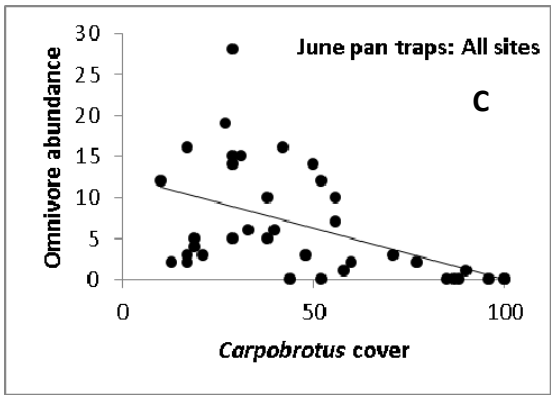
Figure 11. Significant relationships between *Carpobrotus* cover and functional group abundance in March pan traps. MDO = Montaña de Oro, VAN = Vandenberg Air Force Base, and VEN = San Buenaventura State Beach.



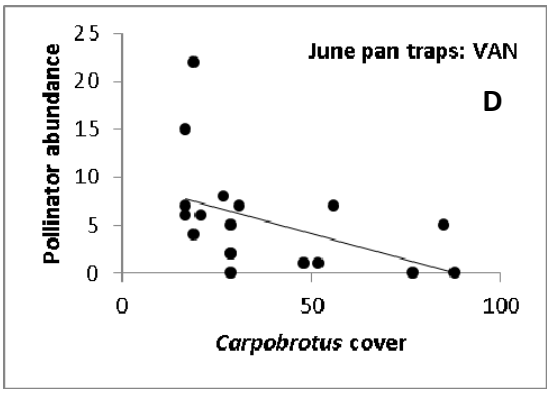
Log (Herb + 1) = 4.57 - 1.19*PlntDiv; Rsquare 0.30, t= -2.56, p=0.02.



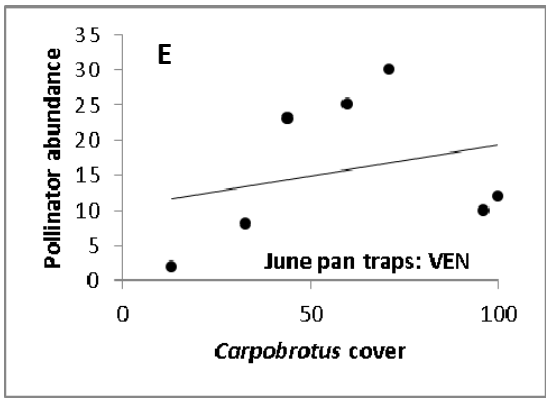
Log (Cicd + 1) = -2.20 + 1.08*log (CAED + 1); Rsquare = 0.39, t= 3.21, p=0.005.



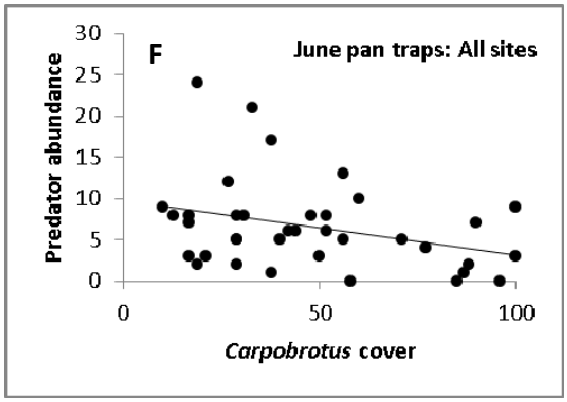
Log (Omn + 1) = 5.12- 0.96*log (CAED + 1); Rsquare = 0.30, t= -3.89, p=0.0004.



Log (Poll + 1) = 5.11 - 1.02*log (CAED + 1); Rsquare = 0.37, t= -3.04, p=0.008.



Log (Poll + 1) = -0.53 + 0.79*log (CAED + 1); Rsquare 0.46, t= 2.07, p=0.09.



Log (Pred + 1) = 3.51 - 0.47*log (CAED + 1); Rsquare 0.13, t= -2.28, p=0.03.

Figure 12. Significant relationships between *Carpobrotus* cover and functional group abundance in June pan traps. MDO = Montaña de Oro, VAN = Vandenberg Air Force Base, and VEN = San Buenaventura State Beach.

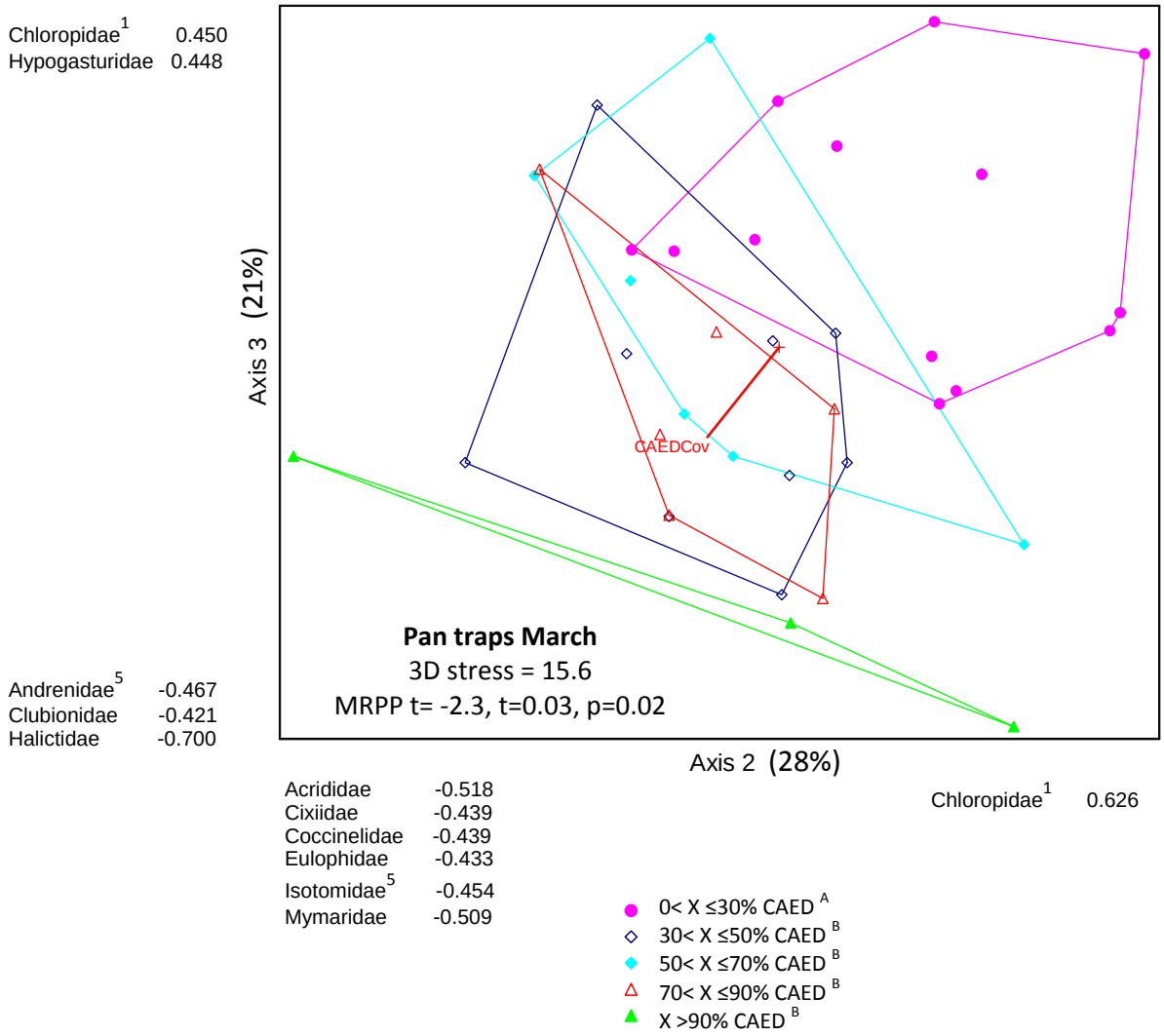


Figure 13. Results of a nonmetric multidimensional scaling (NMDS) analysis applied to the matrix of the relative abundances of all arthropod families in March pan traps, by cover class of *Carpobrotus* plots at all sites. For the 3-dimensional solution, the two axes that explained most of the variation in arthropod taxa by *Carpobrotus* cover class were chosen for this figure. Families correlated with the axes and their Pearson's correlation coefficients are noted in the margins of the diagram; superscripts denote indicator species for 0-30%[1], 30-50%[2], 50-70%[3], 70-90%[4], and >90%[5] *Carpobrotus* cover. Vector indicates the vegetation variable (*Carpobrotus* cover) most associated with the axes. Cover classes significantly different from one another, as indicated by MRPP analysis, are indicated in the legend. Numbers in parentheses indicate the percent variation accounted for by each axis.

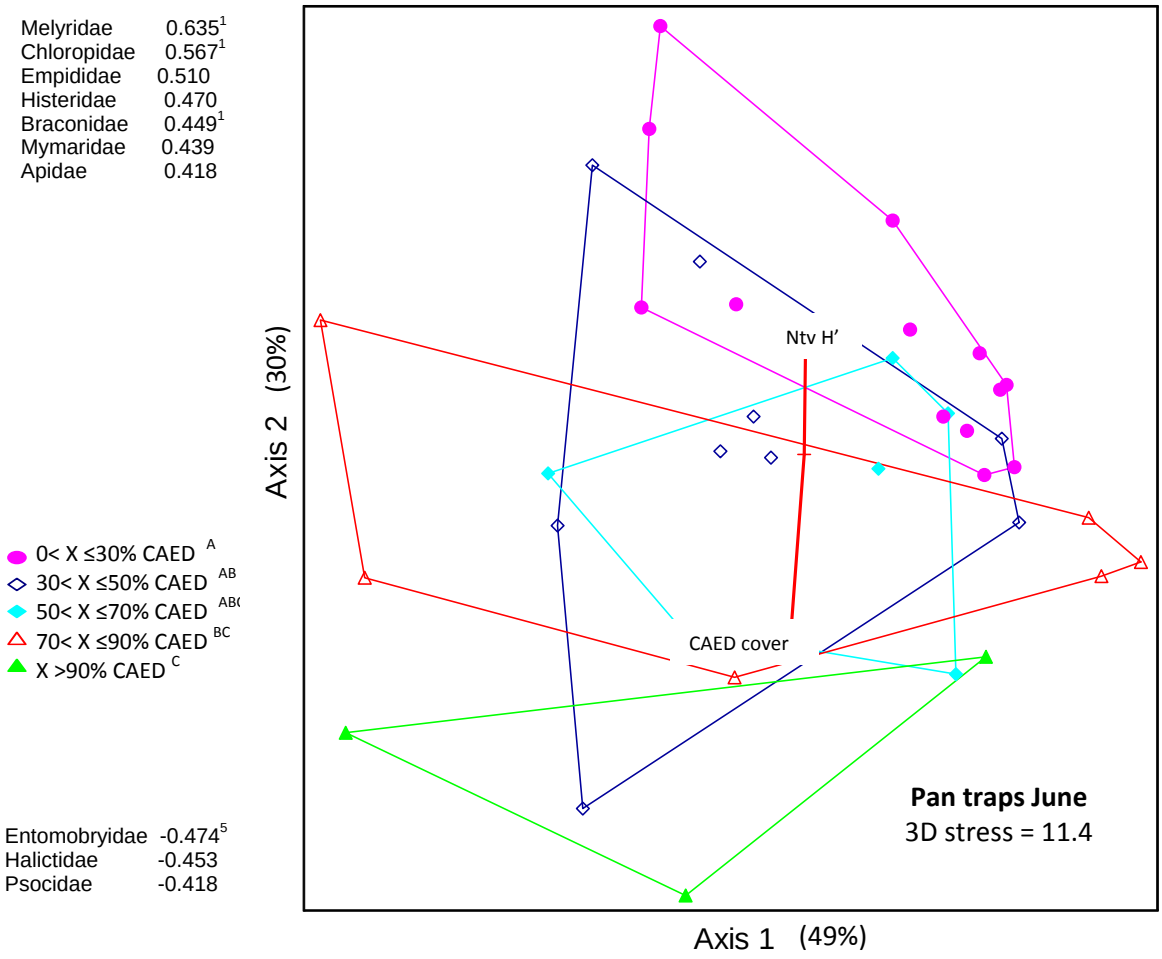


Figure 14. Results of a nonmetric multidimensional scaling (NMDS) analysis applied to the matrix of the relative abundances of all arthropod families in June pan traps, by cover class of *Carpobrotus* plots at all sites. For the 3-dimensional solution, the two axes that explained most of the variation in arthropod taxa by *Carpobrotus* cover class were chosen for this figure. Families correlated with the axis most relevant to *Carpobrotus* cover classes (Axis 2) and their Pearson's correlation coefficients are noted in the margins of the diagram; superscripts denote indicator species for 0-30%[1], 30-50%[2], 50-70%[3], 70-90%[4], and >90%[5] Carpobrotus cover. Vectors indicate the vegetation variables most associated with the axes: *Carpobrotus edulis* cover (CAED) and native plant H' diversity. Cover classes significantly different from one another, as indicated by ANOVA and Tukey's HSD tests with NMDS scores for Axis 2, are indicated in the legend. Numbers in parentheses indicate the percent variation accounted for by each axis.

Supplementary Information, Chapter 2

Table S1. Arthropod taxa found in this study, with their frequency at Montana de Oro (MDO), Vandenberg Air Force Base (VAN), and San Buenaventura State Beach (VEN). Uncommon: <10 individuals collected; occasional: 10-49 individuals collected; common: 50-100 individuals collected; abundant: >100 individuals collected. Specimens were adults unless otherwise noted.

Taxon	Feeding guild	MDO	VAN	VEN
Amphipoda: Talitridae	detritivore	absent	uncommon	absent
Araneae: Agelenidae immature	predator	absent	absent	uncommon
Araneae: Anyphaenidae: *Teudis mordax*	predator	absent	absent	uncommon
Araneae: Araneidae immature	predator	absent	absent	uncommon
Araneae: Clubionidae: *Clubiona* sp.	predator	uncommon	uncommon	uncommon
Araneae: Dictynidae: *Dictyna aggressa*	predator	absent	absent	uncommon
Araneae: Dictynidae: *Dictyna* sp.	predator	absent	uncommon	absent
Araneae: Gnaphosidae: *Herpyllus hesperolus*	predator	uncommon	absent	uncommon
Araneae: Hahniidae immature	predator	absent	uncommon	absent
Araneae: Linyphiidae: *Erigone dentosa*	predator	occasional	occasional	absent
Araneae: Linyphiidae: *Spirembolus* sp.	predator	absent	absent	occasional
Araneae: Liocranidae: *Agroeca*	predator	uncommon	absent	absent
Araneae: Lycosidae: *Pardosa californica*	predator	uncommon	uncommon	absent
Araneae: Megalomorphae unknown	predator	uncommon	occasional	occasional
Araneae: Oonopidae: *Orchestina moaba*	predator	absent	absent	uncommon
Araneae: Philodromidae: *Ebo evansae*	predator	absent	occasional	occasional
Araneae: Phrurolithinae immature	predator	absent	uncommon	absent

Araneae: Salticidae: *Habronattus* sp.	predator	occasional	occasional	occasional
Araneae: Theridiidae: *Crustulina sticta*	predator	absent	uncommon	absent
Araneae: Thomisdae: *Xysticus pretiosus*	predator	uncommon	absent	absent
Blattoidea: Blattelidae	omnivore	uncommon	absent	absent
Chilopoda: Geophilidae	predator	uncommon	uncommon	uncommon
Chilopoda: Lithobiomorpha	predator	absent	absent	uncommon
Coleoptera: Anobiidae: *Ozognathus cornutus*	herbivore	absent	absent	uncommon
Coleoptera: Anobiidae: *Tricorynus*	detritivore	absent	absent	uncommon
Coleoptera: Anthicidae: *Amblyderus parviceps*	detritivore	absent	absent	uncommon
Coleoptera: Anthicidae: *Notoxus*	detritivore	uncommon	uncommon	absent
Coleoptera: Anthribidae: *Ormiscus*	herbivore	absent	absent	uncommon
Coleoptera: Brachypteridae: *Amartus*	herbivore	uncommon	absent	uncommon
Coleoptera: Brentidae: Apioninae	herbivore	uncommon	absent	uncommon
Coleoptera: Buprestidae unknown	omnivore	uncommon	absent	uncommon
Coleoptera: Cantharidae larvae	predator	uncommon	absent	absent
Coleoptera: Carabidae: *Calathus ruficollis*	predator	uncommon	absent	absent
Coleoptera: Chrysomelidae: *Alticini*	herbivore	absent	absent	uncommon
Coleoptera: Chrysomelidae: *Diachus auratus*	herbivore	absent	uncommon	absent
Coleoptera: Cleridae: *Phyllobaenus*	predator	absent	uncommon	uncommon
Coleoptera: Coccinellidae: *Hippodamia convergens*	predator	absent	absent	uncommon
Coleoptera: Coccinellidae: *Hyperaspis quadrioculata*	predator	absent	uncommon	absent

Coleoptera: Coccinellidae: *Scymnus* (2 morphs)	predator	uncommon	absent	absent
Coleoptera: Corylophidae: *Aenigmaticum californicum*	detritivore	uncommon	absent	uncommon
Coleoptera: Cryptophagidae: *Cryptophagous*	detritivore	uncommon	absent	absent
Coleoptera: Curculionidae: *Trigonoscuta*	herbivore	uncommon	uncommon	uncommon
Coleoptera: Dermestidae: *Trogoderma sternale*	detritivore	uncommon	absent	uncommon
Coleoptera: Elateridae: *Cardiophorus*	predator	uncommon	uncommon	uncommon
Coleoptera: Histeridae: *Geomysaprinus*	predator	uncommon	uncommon	absent
Coleoptera: Histeridae: *Hypococcus lucidulus*	predator	absent	uncommon	uncommon
Coleoptera: Histeridae: *Teretrius*	predator	absent	uncommon	absent
Coleoptera: Latridiidae: *Corticarina*	detritivore	absent	uncommon	uncommon
Coleoptera: Leiodidae: *Agathidium*	detritivore	absent	absent	uncommon
Coleoptera: Leiodidae: *Ptomophagous*	detritivore	uncommon	uncommon	absent
Coleoptera: Melyridae: Dastytinae	omnivore	abundant	abundant	abundant
Coleoptera: Mordellidae: *Mordella*	herbivore	uncommon	absent	absent
Coleoptera: Mordellidae: *Mordellistena*	herbivore	uncommon	absent	uncommon
Coleoptera: Ptiliidae: *Acrotrichus*	detritivore	uncommon	absent	uncommon
Coleoptera: Scarabaeidae: *Aegialea*	detritivore	absent	absent	uncommon
Coleoptera: Scarabaeidae: *Hoplia*	herbivore	absent	uncommon	absent
Coleoptera: Scarabaeidae: *Serica*	herbivore	uncommon	absent	uncommon
Coleoptera: Scarabaeidae: *Tesarius*	detritivore	uncommon	uncommon	uncommon

Coleoptera: Silphidae pupa	detritivore	absent	uncommon	absent
Coleoptera: Staphylinidae: *Aleocharinae*	predator	uncommon	uncommon	uncommon
Coleoptera: Staphylinidae: *Medon*	predator	uncommon	uncommon	absent
Coleoptera: Staphylinidae: *Sepedophilus*	predator	uncommon	absent	absent
Coleoptera: Staphylinidae: *Tachyporus*	predator	uncommon	absent	absent
Coleoptera: Tenebrionidae: *Apocrypha anthicoides*	detritivore	uncommon	absent	absent
Coleoptera: Tenebrionidae: *Coelus ciliatus*	detritivore	occasional	common	abundant
Coleoptera: Tenebrionidae: *Eleodes* (2 spp.)	detritivore	absent	uncommon	absent
Coleoptera: Tenebrionidae: *Eleodes nigropilosus*	detritivore	absent	absent	uncommon
Coleoptera: Tenebrionidae: *Helops* (2 spp.)	detritivore	uncommon	absent	uncommon
Collembola: Entomobryidae	detritivore	occasional	uncommon	common
Collembola: Hypogasturidae	detritivore	absent	occasional	absent
Collembola: Isotomidae	detritivore	occasional	uncommon	abundant
Collembola: Sminthuridae	detritivore	uncommon	uncommon	absent
Diplopoda: Chordeumida	detritivore	uncommon	absent	absent
Diplopoda: Spirostreptida	detritivore	uncommon	absent	uncommon
Diptera: Agromyzidae	herbivore	abundant	abundant	abundant
Diptera: Anthomyzidae	detritivore	occasional	uncommon	occasional
Diptera: Asilidae	predator	uncommon	uncommon	uncommon
Diptera: Bombyliidae	parasitoid, pollinator	uncommon	absent	uncommon
Diptera: Cecidomyiidae	non-feeding	occasional	occasional	common
Diptera: Ceratopogonidae	parasite	uncommon	absent	uncommon
Diptera: Chironomidae	non-feeding	absent	uncommon	uncommon

Diptera: Chloropidae: Oscinellinae	detritivore	occasional	abundant	common
Diptera: Conopidae	parasite	absent	uncommon	uncommon
Diptera: Dolichopodidae	predator	uncommon	uncommon	uncommon
Diptera: Empidiidae	predator	abundant	common	abundant
Diptera: Ephydridae	detritivore	uncommon	absent	uncommon
Diptera: Heleomyzidae	detritivore	occasional	occasional	common
Diptera: Lauxaniidae	detritivore	uncommon	absent	uncommon
Diptera: Lonchopteridae	unknown/nectar	uncommon	absent	uncommon
Diptera: Phoridae	detritivore	occasional	uncommon	occasional
Diptera: Sarcophagidae	nectar	occasional	uncommon	occasional
Diptera: Scathophagidae	predator	uncommon	uncommon	uncommon
Diptera: Sciaridae	detritivore	uncommon	occasional	uncommon
Diptera: Sepsidae	detritivore	uncommon	absent	absent
Diptera: Tachinidae	parasitoid, pollinator	occasional	uncommon	occasional
Diptera: Tephritidae	herbivore,scavenger	absent	uncommon	uncommon
Diptera: Therevidae	detritivore	uncommon	occasional	occasional
Hemiptera: Anthocoridae	predator	uncommon	absent	uncommon
Hemiptera: Aphididae	herbivore	occasional	uncommon	abundant
Hemiptera: Cercopidae	herbivore	occasional	uncommon	occasional
Hemiptera: Cicadellidae	herbivore	common	abundant	abundant
Hemiptera: Cixiidae	herbivore	uncommon	absent	absent
Hemiptera: Coccoidea	herbivore	uncommon	absent	uncommon
Hemiptera: Delphacidae	herbivore	uncommon	absent	uncommon
Hemiptera: Fulgoroidea immature	herbivore	occasional	absent	occasional
Hemiptera: Lygaeidae	herbivore	absent	absent	uncommon
Hemiptera: Miridae	herbivore	uncommon	uncommon	uncommon
Hemiptera: Ortheziidae	herbivore	absent	absent	uncommon

Hemiptera: Pentatomidae	herbivore (primarily)	uncommon	absent	uncommon
Hemiptera: Pseudococcidae	herbivore	uncommon	absent	absent
Hemiptera: Reduviidae	predator	absent	absent	uncommon
Hemiptera: Saldidae	predator	absent	absent	uncommon
Hymenoptera: Andrenidae	pollinator	uncommon	absent	occasional
Hymenoptera: Aphelinidae	parasitoid	occasional	uncommon	occasional
Hymenoptera: Apidae: *Apis mellifera*	pollinator	uncommon	uncommon	uncommon
Hymenoptera: Apidae: *Bombus*	pollinator	uncommon	uncommon	uncommon
Hymenoptera: Apidae: *Ceratina*	pollinator	abundant	occasional	common
Hymenoptera: Bethylidae	parasitoid	occasional	absent	uncommon
Hymenoptera: Braconidae	parasitoid	uncommon	uncommon	occasional
Hymenoptera: Ceraphronidae	parasitoid	uncommon	absent	uncommon
Hymenoptera: Chalcididae	parasitoid	uncommon	uncommon	uncommon
Hymenoptera: Chrysididae	parasitoid	uncommon	absent	absent
Hymenoptera: Colletidae: *Hylaeus*	pollinator	occasional	uncommon	occasional
Hymenoptera: Cynipidae	non-feeding	absent	uncommon	uncommon
Hymenoptera: Diapriidae	parasitoid	uncommon	absent	uncommon
Hymenoptera: Dryinidae	parasitoid	uncommon	absent	uncommon
Hymenoptera: Encyrtidae	parasitoid	occasional	uncommon	occasional
Hymenoptera: Eulophidae	parasitoid	occasional	uncommon	occasional
Hymenoptera: Eurytomidae	parasitoid	uncommon	absent	uncommon
Hymenoptera: Formicidae: *Camponotus*	omnivore	occasional	absent	absent
Hymenoptera: Formicidae: *Crematogaster*	detritivore, predator	occasional	occasional	absent
Hymenoptera: Formicidae: *Dorymyrmex*	detritivore	absent	absent	uncommon
Hymenoptera: Formicidae: *Formica*	omnivore	occasional	absent	absent

Hymenoptera: Formicidae: *Hypoponera*	predator	uncommon	absent	absent
Hymenoptera: Formicidae: *Linepithema*	detritivore, predator	uncommon	absent	uncommon
Hymenoptera: Formicidae: *Monomorium*	detritivore, predator	uncommon	absent	absent
Hymenoptera: Formicidae: *Solenopsis*	herbivore, predator	absent	absent	uncommon
Hymenoptera: Formicidae: *Tapinoma*	detritivore	occasional	uncommon	absent
Hymenoptera: Formicidae: *Temnothorax*	omnivore	uncommon	absent	absent
Hymenoptera: Halictidae: *Agapostemon*	pollinator	absent	absent	occasional
Hymenoptera: Halictidae: *Lasioglossum*	pollinator	abundant	common	abundant
Hymenoptera: Halictidae: *Sphecodes*	pollinator	absent	uncommon	abundant
Hymenoptera: Ichneumonidae	parasitoid	uncommon	uncommon	occasional
Hymenoptera: Megachilidae unknown	pollinator	uncommon	absent	uncommon
Hymenoptera: Megachilidae: *Osmia*	pollinator	uncommon	absent	absent
Hymenoptera: Mymaridae	parasitoid	common	occasional	occasional
Hymenoptera: Perilampidae	parasitoid	uncommon	absent	uncommon
Hymenoptera: Pompilidae	predator	occasional	occasional	occasional
Hymenoptera: Proctotrupidae	parasitoid	uncommon	absent	uncommon
Hymenoptera: Pteromalidae	parasitoid	occasional	occasional	occasional
Hymenoptera: Sphecidae	predator	common	uncommon	common
Hymenoptera: Tenthredinidae	herbivore	absent	uncommon	uncommon
Hymenoptera: Tiphiidae	parasitoid	absent	absent	occasional
Hymenoptera: Torymidae	parasitoid	occasional	uncommon	occasional
Hymenoptera: Trichogrammatidae	parasitoid	uncommon	absent	uncommon

Hymenoptera: Vespidae	predator	uncommon	absent	uncommon
Isopoda: Oniscoidea	detritivore	occasional	uncommon	occasional
Isoptera: Rhinotermitidae	herbivore	absent	absent	uncommon
Lepidoptera: Gelechiidae: *Aristotelia argentifera*	pollinator	absent	uncommon	absent
Lepidoptera: Gelechiidae spp.	pollinator	uncommon	absent	absent
Lepidoptera: Gelechioidea spp.	pollinator	uncommon	uncommon	uncommon
Lepidoptera: Geometridae: *Perizoma custodiata*	pollinator	absent	absent	uncommon
Lepidoptera: Geometridae spp.	pollinator	uncommon	uncommon	uncommon
Lepidoptera; Heleodinidae: *Lithanapteryx elegans*	pollinator	uncommon	occasional	absent
Lepidoptera: Nepticulidae?	pollinator	uncommon	absent	absent
Lepidoptera: Plutellidae: *Plutella xylostella*	pollinator	absent	absent	uncommon
Lepidoptera: Pterophoridae sp.	pollinator	absent	uncommon	absent
Lepidoptera: Tortricidae: *Argyrotaenia* sp.	pollinator	absent	uncommon	absent
Lepidoptera: Tortricidae: Cochylinae	pollinator	absent	absent	uncommon
Lepidoptera: Tortricidae spp.	pollinator	uncommon	absent	uncommon
Microcoryphia: Machilidae	detritivore	uncommon	uncommon	occasional
Microcoryphia: Meinertellidae	detritivore	absent	uncommon	occasional
Neuroptera: Myrmeliontidae larva	predator	uncommon	absent	absent
Opiliones unknown	predator	uncommon	absent	absent
Orthoptera: Acrididae	herbivore	uncommon	uncommon	uncommon
Orthoptera: Anostostomatidae	omnivore	uncommon	absent	absent
Orthoptera: Rhaphidophoridae	omnivore	uncommon	uncommon	uncommon
Orthoptera: Romaliidae	herbivore	uncommon	uncommon	absent
Orthoptera: Stenopelmatidae	detritivore	absent	uncommon	absent
Orthoptera: Tettigoniidae	omnivore	uncommon	absent	absent

Pseudoscorpionida	predator	uncommon	uncommon	absent
Psocoptera: Epipsocidae	detritivore	absent	absent	uncommon
Psocoptera: Psocidae	herbivore	absent	uncommon	uncommon
Psocoptera: Trogiidae	detritivore	uncommon	uncommon	uncommon
Thysanoptera: Thripidae	herbivore	abundant	abundant	abundant
Thysanura: Lepismatidae	detritivore	occasional	occasional	occasional

Table S2. Results of ANCOVA analyses examining relationships between arthropod parameters (dependent variables) and site / *Carpobrotus edulis* (CAED) cover (independent variables). For each pair of variables, the table shows significant relationships and associated equations resulting from ANCOVA and linear regression models. Site * CAED data are only presented where significant. Coefficients of determination (R^2), F values, and associated probabilities for final models are shown. MDO= Montaña de Oro, VAN = Vandenberg, VEN = Ventura.

Sample	Dependent var.	Independent var.	MDO LS Mean	VAN LS Mean	VEN LS Mean	Equation	R^2	$F_{1\text{-}2,36}$	P
March soil	Richness[1]	Site, CAED[1]							NS
March soil	Abundance[1]	Site, CAED[1]							NS
March soil	Detritivores[1]	Site	0.39[A]	0.40[A]	1.71[B]			11.1	0.0002
March soil	Detritivores[1]	CAED[1]				See text, Figure 10		3.0	0.095
March soil	Predators[1]	Site, CAED[1]							NS
June soil	Richness[1]	Site	1.32[A]	1.72[B]	2.12[B]			8.8	0.0009
June soil	Richness[1]	CAED[1]							NS
June soil	Richness[1]	Site * CAED[1]						3.4	0.05
		MDO				log (Rich + 1) = -0.65 + 0.53*log (CAED + 1)	0.41	2.64	0.02
		VAN				log (Rich + 1) = 0.73 + 0.27*log (CAED + 1)	0.15	1.71	0.11
		VEN				log (Rich + 1) = 3.05 - 0.25*log (CAED + 1)	0.14	-0.91	0.41

June soil	Abundance[1]	Site	1.55[A]	2.00[A]	2.68[B]			8.2	0.001
June soil	Abundance[1]	CAED[1]							NS
June soil	Detritivores[1]	Site	0.72[A]	1.30[AB]	1.72[B]			4.8	0.02
June soil	Detritivores[1]	CAED[1]							NS
June soil	Predators[1]	Site, CAED[1]				See text, Figure 10			NS
March pan	Abundance[1]	Site	3.26[AB]	2.86[A]	3.42[B]			4.67	0.02
March pan	Abundance[1]	CAED[1]				See text, Figure 9		6.32	0.02
March pan	Richness	Site, CAED[1]							NS
March pan	Detritivores[1]	Site, CAED[1]							NS
March pan	Detritivores[1]	Site * CAED[1]						4.4	0.02
		MDO				log (detr + 1) = -0.72 + 0.55*log (CAED + 1)	0.22	1.7	0.12
		VAN				log (detr + 1) = 4.97 - 0.94*log (CAED + 1)	0.32	-2.77	0.01
		VEN				log (detr + 1) = -0.15 + 0.24*log (CAED + 1)	0.03	0.38	0.72
March pan	Herbivores[1]	Site							NS
March pan	Herbivores[1]	CAED[1]				See text, Figure 11		7.4	0.01
March pan	Herbivores[1]	Site * CAED[1]						4.1	0.03
		MDO				Log (herb + 1) = 3.39 -	0.14	-1.27	0.23

							0.30*log (CAED + 1)			
			VAN				Log (herb + 1) = 1.72 + 0.037*log (CAED + 1)	0.00	0.15	0.89
			VEN				Log (herb + 1) = 6.96 - 1.31*log (CAED + 1)	0.47	-2.09	0.09
	March pan	SpecHerbivores[1]	Site	0.85[A]	0.80[A]	1.71[B]			4.2	0.02
	March pan	SpecHerbivores[1]	CAED[1]				See text, Figure 11		3.8	0.06
	March pan	SpecHerbivores[1]	Site * CAED[1]						4.2	0.005
			MDO				log (cicd + 1) = -0.10 + 0.26*log (CAED + 1)	0.05	0.72	0.49
			VAN				log (cicd + 1) = 0.66 + 0.03*log (CAED + 1)	0.00	0.13	0.90
			VEN				log (cicd + 1) = 7.36 - 1.52*log (CAED + 1)	0.68	-3.28	0.02
	March pan	Parasitoids[1]	Site	1.41[A]	0.63[B]	0.95[AB]			4.4	0.02
	March pan	Parasitoids[1]	CAED[1]							NS
	March pan	Pollinators[1]	Site, CAED[1]							NS
	March pan	Pollinators[1]	Site * CAED[1]						5.2	0.01
			MDO				log (poll + 1) = 1.31 + 0.07*log (CAED + 1)	0.00	0.11	0.91
			VAN				log (poll + 1) = 3.04 - 0.48*log (CAED + 1)	0.18	-1.86	0.08
			VEN				log (poll + 1) = -4.15 + 1.43*log (CAED + 1)	0.86	5.63	0.002

March pan	Predators[1]	Site	0.50[A]	0.69[A]	1.80[B]			13.1	<0.0001
March pan	Predators[1]	CAED[1]				See text, Figure 11		5.5	0.03
March pan	Predators[1]	Site, CAED[1]						3.6	0.04
June pan	Richness	Site							NS
June pan	Richness	CAED[1]				y=31.3 – 3.4x	0.17	-2.7	0.01
June pan	Abundance[1]	Site	3.81[A]	4.50[B]	4.44[B]			7.3	0.003
June pan	Abundance[1]	CAED[1]							NS
June pan	Detritivores[1]	Site, CAED[1]							NS
June pan	Herbivores[1]	Site	2.31[A]	3.98[B]	3.34[AB]			11.2	0.0002
June pan	Herbivores[1]	CAED[1]							NS
June pan	SpecHerbivores[1]	Site	0.45[A]	1.83[B]	0[A]			27.7	<0.0001
June pan	SpecHerbivores[1]	CAED[1]							NS
June pan	SpecHerbivores[1]	Site * CAED[1]						5.9	0.007
		MDO				log (Cicd + 1) = 1.36 - 0.25*log (CAED + 1)	0.09	-1.02	0.33
		VAN				log (Cicd + 1) = -2.20 + 1.08*log (CAED + 1)	0.39	3.21	0.005
		VEN				(no Cicadellidae)			
June pan	Omnivores[1]	Site							NS
June pan	Omnivores[1]	CAED[1]				y=5.1 – 0.96x	0.30	10.4	0.003
June pan	Parasitoids[1]	Site	0.92[A]	1.38[AB]	1.55[B]			4.2	0.02

June pan	Parasitoids[1]	CAED[1]							NS
June pan	Pollinators[1]	Site	2.11[A]	1.29[B]	2.42[A]			7.6	0.002
June pan	Pollinators[1]	CAED[1]							NS
June pan	Pollinators[1]	Site * CAED[1]						6.9	0.003
		MDO				log (Poll + 1) = 1.478 + 0.17 *log (CAED + 1)	0.03	0.52	0.61
		VAN				log (Poll + 1) = 5.11 - 1.02*log (CAED + 1)	0.37	-3.04	0.008
		VEN				log (Poll + 1) = -0.53 + 0.79*log (CAED + 1)	0.46	2.07	0.09
June pan	Predators[1]	Site							NS
June pan	Predators[1]	CAED[1]				y=3.5 – 0.47x	0.13	5.24	0.03
June pan	Predators[1]	Site * CAED[1]							NS

[1] Log (X+1) transformed

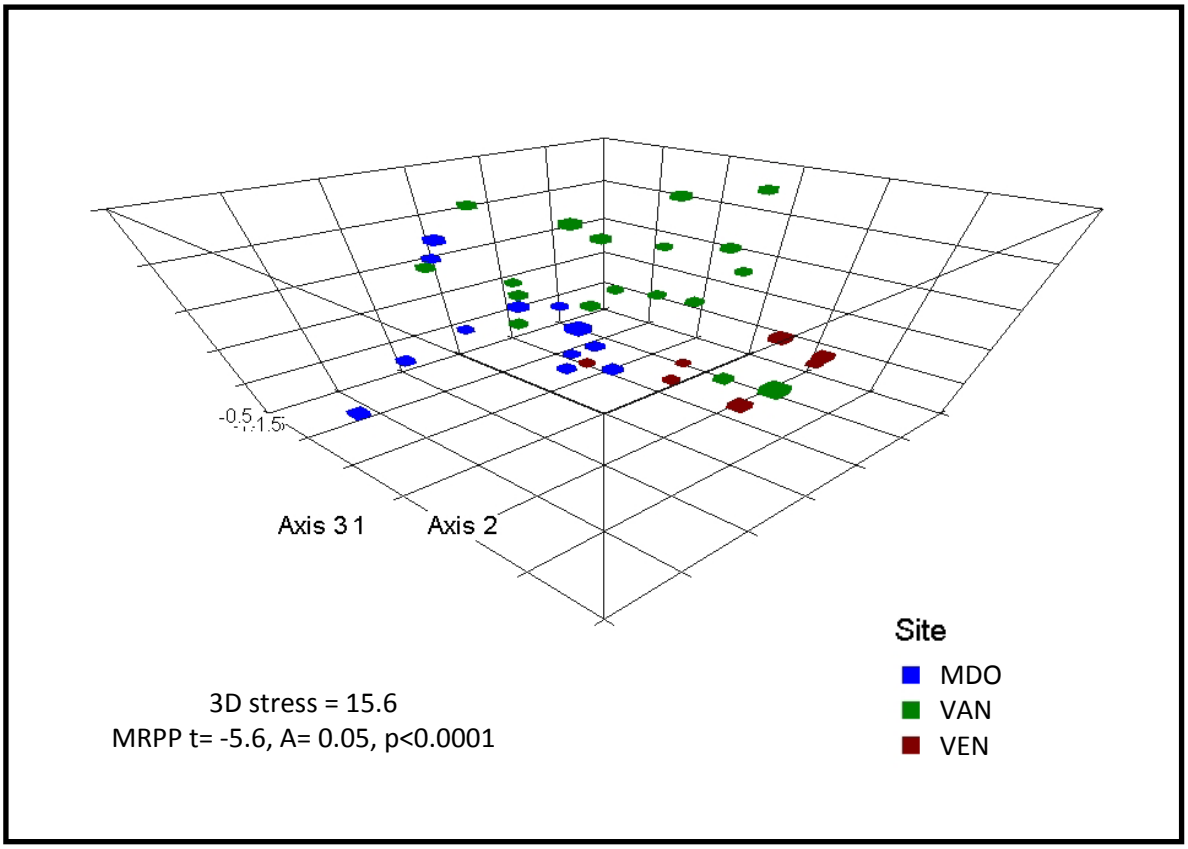


Figure S1. Results of a nonmetric multidimensional scaling (NMDS) analysis applied to the matrix of the relative abundances of all arthropod families in *Carpobrotus* plots of March pan traps, by site (MDO = Montaña de Oro, VAN = Vandenberg Air Force Base, VEN = San Buenaventura). Percent variation accounted for by each axis was 28%, 28%, and 21% for axes 1, 2, and 3 respectively. MRPP analysis indicates that all sites are significantly different from one another.

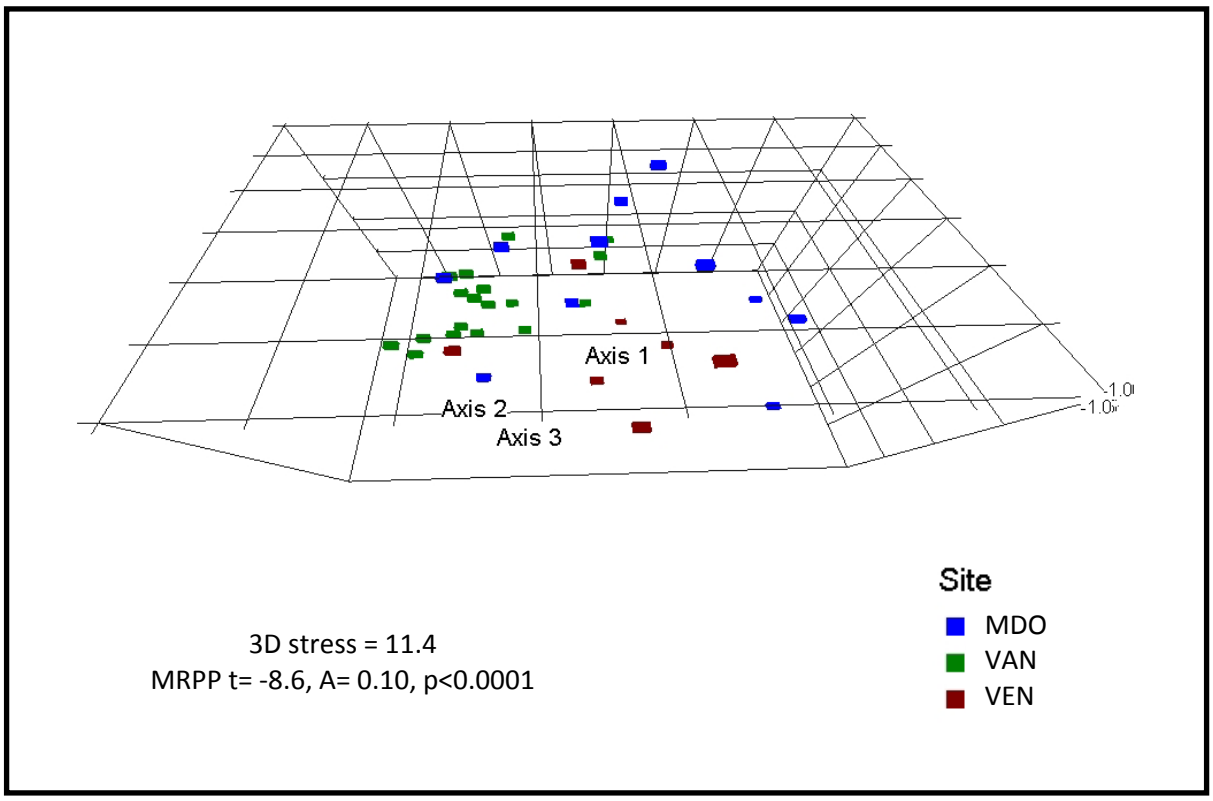


Figure S2. Results of a nonmetric multidimensional scaling (NMDS) analysis applied to the matrix of the relative abundances of all arthropod families in *Carpobrotus* plots of June pan traps, by site (MDO = Montaña de Oro, VAN = Vandenberg Air Force Base, VEN = San Buenaventura). Percent variation accounted for by each axis was 49%, 30%, and 10% for axes 1, 2, and 3 respectively. MRPP analysis indicates that all sites are significantly different from one another.

CHAPTER 3

EXPERIMENTAL RESTORATION REVEALS EFFECTS OF INCREASING *CARPOBROTUS EDULIS* DOMINANCE AND DECREASING PLANT DIVERSITY ON COASTAL DUNE ARTHROPODS

Abstract: Invader abundance is often assumed to contribute to the impact of an invasive species, but few studies have examined this relationship, with those few producing inconsistent results. Additionally, considering feeding guilds across an entire arthropod assemblage will help to identify mechanisms and patterns, and begin to link impacts on community structure to ecosystem processes. In this study, I used an experimental restoration approach to investigate how arthropod assemblages responded to a constructed gradient of *Carpobrotus edulis* abundance in a coastal dune native plant matrix. Arthropods were sampled in March and June of 2013 using both sand sifting and pan trapping techniques, sorted to morphospecies by family, and assigned to one of six primary feeding guilds. Arthropod abundance decreased exponentially with increasing *Carpobrotus* cover in March and June soil samples and in March pan traps, and decreased linearly in June when thrips, which were abundant and highly associated with *Carpobrotus,* were excluded. Detritivores and thrips pan trapped in June were the only groups, techniques, and times to show positive associations with *Carpobrotus* invasion. All other groups except for pollinators decreased with increasing *Carpobrotus* cover in at least one sampling period. Fossorial detritivore and predator taxa were most negatively affected, perhaps due to dense *Carpobrotus* roots which pose a barrier. Herbivores in March and

omnivores, parasitoids, and predators in June were largely responsible for the above-ground decrease observed. Across sampling techniques and times I found a general change in arthropod composition between *Carpobrotus* control plots and 1/3 native plots vs. 2/3 native, 3/3 native, and remnant native plots, driven by *Carpobrotus* dominating in the former two treatments and increased H' diversity in the latter three treatments. The soil and March pan trap data indicated that arthropod communities converged to natural configurations within a few years after *Carpobrotus* was removed and replaced with native vegetation, while the June pan trap data indicated that there were still differences between restored and natural areas. The dramatic decline observed at low invader abundance has negative implications for higher trophic levels and ecosystem functions. Quantitative knowledge of relationships between invader abundance and impact will guide efforts to preserve and restore native diversity.

Introduction

Although invasive species can have pervasive effects on native communities and ecosystems, there is inadequate knowledge of the relative contributions of, and interactions among, key factors determining invader impacts (Thomsen et al. 2011). Among these factors is invader abundance, often quantified as percent cover, which is often assumed to determine invader impact (e.g., Parker et al. 1999; Ricciardi 2003; Thiele et al. 2010). Few studies have examined this relationship, however, with those few producing inconsistent results. A few local-scale studies have indicated that both arthropod and bird

richness increased between zero and ~50% invader cover, then declined at higher cover levels (Van Riper et al. 2008; Almeida-Neto et al. 2011). Almeida-Neto et al. (2011) linked arthropod richness responses to plant invasions to changes in resident plant diversity, while Van Riper et al. (2008) hypothesized that changes in bird richness were caused both by changes to structural complexity of vegetation, which was highest at intermediate invader densities, and arthropod abundance, which decreased at high cover values of the invader. Other studies have found a negative linear relationship between arthropod diversity and invader cover, and linked arthropod diversity declines to decreasing plant diversity (e.g., Schooler et al. 2009; Spyreas et al. 2010). One study reported an exponential decrease in arthropod abundance with increasing cover of an invasive plant, which was hypothesized to be related to the stabilization of dune soils at high invader densities (Slobodchikoff and Doyen 1977).

Community-level abundance-impact patterns are likely to be heavily influenced by the trophic level and functional group of the residents. Arthropods constitute a dominant component of biodiversity and perform a variety of important ecological functions (pollination, decomposition, and regulation of plant and animal populations) (Gullan and Cranston 2005). Although biologists are increasingly examining arthropod responses to non-native plant invasions (e.g., Dibble et al. 2013, van Hengstum et al. 2014), most past studies have focused on a narrow array of species, rarely considering entire arthropod assemblages with species fulfilling many functional and trophic roles (Harvey et al. 2010; Bezemer et al. 2014). An analysis across all arthropod groups will help quantify and

delineate the mechanisms for the effects of plant invasions on entire communities, and begin to link impacts on community structure to ecosystem processes (Levine and D'Antonio 2003).

Herbivores, particularly specialists, are often more negatively affected than other feeding guilds by introduced plants (Kappes et al. 2007; Proches et al. 2008; Hartley et al. 2010), This could be due to these plants having physical and chemical characteristics to which resident herbivores are not adapted (Strong et al. 1984; Haynes and Cronin 2003; Kuhnle and Muller 2009). Predators and parasitoids both benefit from a greater diversity and complexity of plants and habitats, because this provides them with a greater abundance or diversity of prey, hosts, or alternative food resources, as well as perch sites (Langellotto and Denno 2004; Scherber et al. 2010; Price et al. 2011). Pollinators form a continuum from extreme specialists on one hand, with one pollinator depending on one plant, to broad generalists (Johnson and Steiner 2000), and their abundance can decrease if invaders lower plant diversity (Valtonen et al. 2006; Moron et al. 2009). Lastly, detritivores may benefit from the high biomass, growth, and production of many successful invasive plants (Liao et al. 2008; Grotkopp et al. 2010), which produce dense plant litter accumulated over successive growth cycles (Holdredge and Bertness 2011; Topp et al. 2008; Moron et al. 2009).

In this study, I used an experimental restoration approach to investigate how arthropod assemblages respond to three different levels of invasive plant abundance in a native plant matrix. I conducted this study in a central coast dune system in California

dominated by *Carpobrotus edulis* (highway ice plant, Hottentot fig), a South African plant introduced to California around the turn of the 20th century and now found along the state's entire coastline (Albert 1995, 2000). *Carpobrotus* is phylogenetically distinct because it is in the Aizoaceae and only one native member of the Aizoaceae occurs in coastal California (Hickman 1993). Owing to its dense, fibrous root system, mat-like growth form, and high production and biomass (D'Antonio and Mahall 1991), *C. edulis* stabilizes highly mobile coastal dunes, suppresses the growth and abundance of native plants, and generates large amounts of living and dead organic matter (D'Antonio 1993; Albert 1995, 2000; Campos et al. 2004; Vila et al. 2006; Molinari et al. 2007). *Carpobrotus edulis* also alters its local environment, reducing soil pH and increasing salinity and organic matter (Albert 1995; Vila et al. 2006; Molinari et al. 2007; Conser and Connor 2009; Novoa et al. 2012, 2013).

I examined the responses of arthropod abundance, richness, feeding guild abundances, and species composition to a constructed gradient of non-native and native plant cover. I predicted declining arthropod abundance and richness as *Carpobrotus* cover increased, and altered species composition. I also expected that arthropod herbivores, omnivores, parasitoids, predators, and pollinators would decrease in abundance with *Carpobrotus* invasion due to a decrease in plant diversity, but that detritivores would become more abundant with increasing *Carpobrotus* cover associated with increasing plant litter.

Methods

Site descriptions

This experiment was conducted in the western portion of the University of California's Coal Oil Point Reserve (Santa Barbara County, California, lat. 34°24.8' N, long. 119°53.0' W), where approximately one hectare of coastal dunes dominated by *Carpobrotus edulis* was located next to dunes dominated by native plant species. Dominant native plant species in the dunes include *Ambrosia chamissonis*, *Abronia maritima, Abronia umbellata*, and *Camissonia cheiranthifolia*. Precipitation at this location ranges from 36 to 53 cm per year and average temperatures range from a 6° C minimum in January to a 24° C maximum in August (Coal Oil Point Reserve data).

Sampling design

In January of 2010, eight 7x7 meter plots were established randomly within *Carpobrotus*-dominated and adjacent native-dominated dunes (hereafter referred to as the "intact" treatment). These sixteen (8 per habitat) plots were sampled for arthropods in February and May of 2010 to provide pre-manipulation data on arthropod communities. Twenty additional plots were established in the *Carpobrotus* (experimental) area that summer and the 28 plots in *Carpobrotus* were assigned to one of four treatments: (a) 1/3 *Carpobrotus* removed and revegetated with native species (1/3 native), (b) 2/3 removal and revegetation, (c) full removal and revegetation (3/3 native), and 4) no removal (100%

Carpobrotus). This resulted in seven replicates for each experimental treatment and eight intact native plots. The farthest of the intact remnant dune plots was dropped from the study to standardize sample sizes, and two experimental plots (one 1/3 native treatment, one 2/3 native treatment) were later excluded because they had different substrata than other plots (Table 1).

Restoration

Within each 7x7 m removal plot, *Carpobrotus* was removed in continuous 2x2 meter subplots. To allow for its rapid growth over the course of the ensuing three years, *Carpobrotus* was removed from distances 0.5 meter beyond the experimental boundary ultimately desired for monitoring of responses. In summer 2010, *Carpobrotus* was severed at the manipulated subplot edges then killed by covering the manipulated area with a black plastic tarp (Horowitz et al. 1983). Following *Carpobrotus* death in fall and winter of 2010, all *Carpobrotus* biomass (including roots) was removed and transported away from experimental plots. Simultaneous with the initiation of *Carpobrotus* control, native plants were started for eventual outplanting to the plots. Eight native dune species, chosen because of their dominance in the community and diversity of morphology and flower color: *Abronia maritima*, *Ambrosia chamissonis*, *Camissonia cheiranthifolia*, *Eriogonum parvifolium*, *Eschscholzia californica*, *Isocoma menziesii*, *Malacothrix saxatilis*, and *Phacelia ramosissima*. These were propagated in fall of 2010 from seed collected from the Reserve. Propagated plants were transplanted into experimental plots in January and February

2011. High mortality of transplanted native plants due to drought conditions necessitated additional plantings in winter of 2012, which included the transplantation of young *Ambrosia* and *Abronia umbellata* from intact dunes to the restoration plots. Colonizing non-natives were periodically weeded, while colonizing and existing natives were allowed to remain; additional species in the re-vegetated plots included *Baccharis pilularis*, *Distichlis spicata*, *Ambrosia psilostachya*, and *Acmispon maritimus*.

Arthropod sampling

Arthropods were sampled in March and June of 2013 using both sand sifting and pan (water) trapping techniques, to capture soil and primarily aerial arthropods, respectively (Southwood 1978). Sampling was conducted in the central 6x6 meter area of each plot to avoid edge effects. Two one-liter soil samples (approximately 12 cm deep) were taken from each of 3 diagonal subplots (total = 6 cores), representing the relative proportions of *Carpobrotus* and native vegetation found in each plot. Core samples were placed in a 1 mm mesh sieve and shaken, retaining larger organisms and debris while also collecting smaller plant material and arthropods in a shallow container, which was as wide and twice as long as the sieve, placed below the sieve. Arthropods were aspirated from the sieve and container until at least five minutes had passed and no arthropods had been collected for two minutes. Arthropod specimens were then preserved in 70% ethanol. Yellow bowls were used as pan traps, because they attract a variety of Diptera, Hymenoptera, and Coleoptera, three of the most taxonomically and ecologically diverse

insect orders (Southwood 1978). An 18 cm bowl filled with water and a few drops of liquid dish soap was placed above-ground in the center of each plot, secured with two wood skewers, then left in place for three days and two nights (60 hours). Arthropods were strained and preserved in 70% ethanol. Arthropod sampling was conducted in March and June of 2013 rather than February and May as in pre-experimental sampling, in order to capture more (and more mature) arthropods.

Vegetation sampling

Vegetation was sampled in March of 2013 using point-intercept transects. Four parallel transects were evenly spaced through the plot. Every half meter along each of these transects (a total of 52 points), the plant species intercepted was recorded along with maximum plant height, substratum (sand or plant litter), litter depth, and the presence/absence as well as identity of flowers present within a 0.5 x 0.5 m quadrat centered on that point. These data were used to calculate percent *Carpobrotus* cover, percent native plant cover, plant Shannon diversity (H') (overall as well as native), species richness, *Carpobrotus* flower density (% points with *Carpobrotus* flowers), non-*Carpobrotus* flower density, average height, coefficient of variation for height, percent standing dead plant cover, and average litter depth for each plot. Although the flower density technique proved inadequate, it is included here to illustrate general changes in flower density with *Carpobrotus* invasion.

Soil and litter measurements

All plant litter remaining in sieves following sampling of soil arthropods was transferred to brown paper bags, air dried, and weighed. Percent soil moisture was calculated by weighing 10 g subsamples of soil, oven drying at 105° C, then re-weighing and calculating % moisture as [(wet weight – dry weight)/(dry weight)] X 100. After sieving remaining soil through 2 mm mesh, 15 mL of de-ionized (DI) water was added to three grams of soil then, after 30 minutes, the salinity and pH of solutions was measured using a Eutech Instruments EC/TDS/Salt tester and an Orion Research digital pH meter (model 611), respectively. Lastly, soil texture was measured by adding 40 g of dry soil to 100mL of Calgon solution (1 L of DI water + 35 g $Na(PO_3)_6$), diluting to 1 L with DI water, suspending all particles using a plunger, then using a Fischer Scientific 11-583 hydrometer to measure specific gravity at both 40 seconds and 7 hours (Gee and Or 2002). Percent sand was calculated as 100 - (hydrometer reading at 40 seconds/dry weight)*100.

Arthropod Identification

All insects were identified at least to the family level, and other arthropods were identified to the finest possible taxonomic level (family or order). Specimens were identified to finer resolution when required for functional group determinations, such as for ants and some Diptera. In addition, most beetle (Coleoptera) specimens were identified to genus or species by a specialist (M. Caterino). All arthropod specimens were sorted to morphospecies (morphologically distinct organisms) within each vial for richness estimates

(Oliver & Beattie 1996; Derraik et al. 2002). For use with rarefaction analyses, morphospecies were assigned ID's and tracked across all samples for three of the most abundant and functionally diverse insect orders (Coleoptera, Hymenoptera, and Diptera), using pinned specimens where possible as well as photographs and drawings of key characteristics.

Arthropod identification followed Triplehorn and Johnson (2005) for most taxa, but Arnett and Thomas (2001) was used for Coleoptera and Smith and Carlton (1975) was used for isopods. Spider specimens from 2010 were identified by a specialist (Dr. R. Vetter, University of Riverside). I was unable to identify mites to family, and thus could not include them in the functional group analyses. This is not expected to change the results because, on average, less than one mite was collected per plot.

Functional groups

Taxa (and their developmental stages) were assigned to one of six primary feeding guilds (detritivore, herbivore, omnivore, parasitoid, pollinator, and predator) using McAlpine et al. (1981), McAlpine et al. (1987), Arnett and Thomas (2001), Arnett et al. (2002), and Triplehorn & Johnson (2005). The detritivore group included coprophages, fungivores and scavengers, as all of these groups utilize organic material either directly or indirectly in its decomposing state. Although many insects visit flowers to obtain nectar, only those taxa considered classic pollinators were classified as such: adult bees, butterflies and moths, and selected fly families (Acroceridae, Bombyliidae, Muscidae, Syrphidae and

Tachinidae) (Mader et al. 2011). For soil samples, only the two most abundant functional groups were analyzed (detritivores and predators), because specimens of other guilds were uncommon. For taxa known to have two distinct feeding habits within either the immature or adult life stage, each feeding guild was assigned a value of 0.5 for each individual.

Statistical analyses

Vegetation attributes were compared among treatments using one-way ANOVAs, followed by t-tests or (where parametric assumptions could not be met) Wilcoxon rank sum tests on all treatment pairs, with corrections for comparisonwise error across treatments using the False Discovery Rate procedure (Benjamini & Hochberg 1995). Variables were log (x+1) transformed when necessary to meet parametric test assumptions. Arthropod abundance was compared between months by treatment using t-tests or Wilcoxon rank sum tests.

Experimental manipulations created a final gradient of *Carpobrotus* cover and native plant diversity, so I primarily analyzed the arthropod data using independent variables that were continuous rather than categorical. Both linear regression and curve-fitting procedures were performed using arthropod abundance and richness as the dependent variables and *Carpobrotus* cover as the independent variable. I used the Shapiro-Wilk test on residual error terms to test for assumptions of normality, then used log (x + 1) transformations when this assumption was not met. To examine the influence of plant diversity, I also performed both linear and polynomial regression on arthropod

abundance using plant H' diversity as the independent variable. Lastly, to investigate vegetation variables most likely driving individual feeding guild responses, I performed ordinary least-squares regression analysis on the absolute abundance of those feeding guilds and the plant variables hypothesized to drive responses (plant H' diversity, litter biomass). The above analyses were conducted in JMP 10.0 (SAS Institute, Cary, NC).

I performed rarefaction analysis on Coleoptera, Diptera, and Hymenoptera morphospecies numbers in order to determine abundance-adjusted morphospecies richness, in EstimateS software version 9.1 (Colwell 2013). I used the minimum number of individuals of each taxon collected in an individual samples as the fixed number for determining species richness. Rarefaction analysis could not be performed on soil arthropod richness results, even when months were combined, because of low numbers in core samples.

Non-metric multidimensional scaling was used to visualize differences in the relative abundances of collected taxa across treatments for each month and method. In these analyses, I used data on the relative abundances of all arthropod families rather than morphospecies of the three selected orders in order to include all arthropod taxa and to ensure adequate numbers for analysis. It was necessary to combine some samples (February and May soil for 2010, March and June soil for 2013, February and May pan trapped samples for 2010) in order to obtain an ordination solution. I determined the effects of treatment on arthropod community structure using the Multi-Response Permutation Procedure (MRPP) (Mielke and Berry 2001). Sorenson (Bray-Curtis) distance

measures were used for both of these analyses. In addition, Indicator Species Analysis was used to determine the families that were associated with specific treatments based on the concentration of abundance and faithfulness to that treatment (Dufrêne and Legendre 1997). All multivariate analyses were performed using PCOrd software, version 6 (McCune and Mefford 1999).

Results

A total of 8,492 individual arthropods were collected from soil and pan sampling in 2010 and 2013. These represented 20 orders and 121 families (Supplemental Information, Table S1). Over 50% more individuals were captured in June soil than March soil samples (15.3 ± 2.6 SE vs. 9.7 ± 1.5; Wilcoxon rank sum test, $p=0.15$), and nearly 3X more individuals were captured in June pan traps than March pan traps (148.6 ± 7.5 vs. 52.8 ± 7.4 SE; t-test, $t=9.1$, $p<0.0001$). Within the Coleoptera, Hymenoptera, and Diptera, 208 different species and morphospecies were identified.

Percent *Carpobrotus* and native plant cover, plant diversity and richness, native plant diversity, *Carpobrotus* flower density, % dead cover, and average litter depth were significantly different among at least some treatments, in accordance with desired treatment levels, but variation in plant height and native plant flower density were not (Table 1). Average plant height was significantly greater in intact native plant plots than in other plots, owing to the presence and abundance of low-lying *Carpobrotus* in other plots.

Soil moisture, average litter depth, litter biomass, and conductivity, but not % sand or pH, were significantly higher in *Carpobrotus* plots than intact plots (Table 2). Figures 1 and 2 illustrate the gradients that resulted from iceplant control and native re-vegetation, with plant diversity decreasing and plant litter depth increasing, respectively, as *Carpobrotus* cover increased.

Arthropod abundance and richness

Arthropod abundance decreased exponentially with increasing *Carpobrotus* cover in March and June soil samples and in March pan traps (Figure 3). Abundance increased with increasing *Carpobrotus* cover in June pan traps due to a strong positive response by thrips (Thysanoptera: Thripidae) to *Carpobrotus,* but decreased linearly when thrips were excluded (Figure 3). Across sampling periods and methods, abundance was reduced by 70-88% from plots with no *Carpobrotus* to the highest levels of *Carpobrotus* cover.

Treatment differences prior to restoration actions in 2010 and following restoration in 2013 are shown in Figure 4. Soil arthropods were less abundant in *Carpobrotus* plots than in intact native plots in both February and May prior to restoration actions, as well as in March and June 2013 following restoration. Following *Carpobrotus* removal and re-vegetation in 2013, 1/3 native plots had similar soil arthropod abundance to high *Carpobrotus* plots, while 2/3 and 3/3 native plots were intermediate between high *Carpobrotus* and intact plots in both months. In pan traps, *Carpobrotus* plots had slightly but significantly greater arthropod abundance than intact native plots in February 2010 but

no significant difference between these treatments in May 2010. Following restoration in 2013, however, intact native plots had significantly more pan-trapped arthropods in both March and June, with experimental plots showing the same pattern as soil samples: 1/3 native plots similar in abundance to high *Carpobrotus* plots, and 2/3 and 3/3 native plots similar to intact native plots. Due to high variance and corrections for many comparisons, differences were not significant in June 2013 and the only significant differences in March were high *Carpobrotus* vs. intact native and 1/3 native vs. intact, 3/3 native, and 2/3 native.

Arthropod morphospecies richness in March and June soil samples and in June pan traps followed abundance patterns, decreasing with increasing *Carpobrotus* cover, by 56 and 89% from the lowest to highest *Carpobrotus* levels in March and June soil samples, and by approximately 36% in June pan traps. Richness in pan traps in March was not related to *Carpobrotus* cover, however. Rarefied arthropod richness data for Coleoptera, Diptera, and Hymenoptera in both March and June pan traps showed no relationship with *Carpobrotus* cover, indicating that richness patterns were driven by abundance.

Arthropod abundance relationships with plant H' diversity were consistently positive (Fig. 5); this was significant for March soil and pan traps and June pan traps, and a trend for June soil. Rsquare and p-values were never as strong as those for arthropod abundance and *Carpobrotus* cover, however.

Arthropod feeding guild abundance

Significant relationships between feeding guilds and *Carpobrotus* abundance are

shown in Figures 6 and 7. Detritivores and thrips pan trapped in June were the only groups, techniques, and times to show positive associations with *Carpobrotus* invasion. In contrast, soil predators (both months), herbivores in March, and pan-trapped omnivores and parasitoids in June decreased with increasing *Carpobrotus* cover. Soil detritivores in both months and pan-trapped predators in June decreased between 0 and ~50% *Carpobrotus* cover, and then increased.

Feeding guild relationships to selected vegetation variables are presented in Table 3. Soil detritivores were negatively related to litter depth in both months (trend only in March), while pan-trapped detritivores were positively related to litter depth in June but not March. Herbivores were positively related to plant H' diversity in March, but negatively related in June, due to thrips; when thrips were excluded, there was no relationship in June. Omnivores and parasitoids were positively related to plant H' diversity in June, but not in March. Soil predators were positively related to plant H' diversity in March and exhibited a trend in this direction in June, while pollinators exhibited this trend in March. Pan-trapped predators had no relationship with plant H' diversity.

Arthropod community structure

NMDS plots for 2010 pre-treatment data (Fig. 8) showed strong separation in arthropod community structure in both soil samples and pan-trapped samples. MRPP analysis corroborates these differences (A's =0.07 and 0.11, p's ≤0.0002). Axes 2 and 1, which were most closely associated with soil and pan traps treatment differences,

respectively, explained 24 and 59% of the variation in relative abundance data. Among soil taxa, rove beetles (Staphylinidae: predators) and woodlice (*Porcellio*, Porcellionidae: detritivores) were most associated with *Carpobrotus* plots, while dune spiders in the genus *Lutica* (Zodariidae: predators), dune beetles (*Coelus ciliatus:* Tenebrionidae: scavengers), multiple native ant genera (Formicidae: various feeding guilds), and termites (Rhinotermitidae: herbivores) preferred native plots. In addition, a significant Indicator Species for Intact plots that was not well correlated with either axis were detritivorous scarab beetles (Scarabaeidae) in the genus *Tesarius*. In pan trapped samples, a variety of detritivorous flies including Heleomyzidae, Scathophagidae, and Anthomyiidae preferred *Carpobrotus* plots, as did thrips (Thripidae: herbivores), Mymaridae (parasitoids), Chironomidae (non-feeding as adults) and two familes of spiders: Lycosidae and Salticidae. In contrast, flower beetles (Melyridae: omnivores), aphids (Aphididae: herbivores), and Pteromalidae (parasitoids) preferred native plots.

NMDS plots for 2013 soil data (Fig. 9) show differences in arthropod community structure between high *Carpobrotus* and, to a lesser extent, 1/3 native plots versus 2/3, 3/3 and intact native plots, with considerable overlap between the three most native treatments. MRPP results show that the strongest treatment differences for soil samples were between high *Carpobrotus* plots and the three most native treatments. Plots from pan traps in March (Fig. 10) show the strongest separation between high *Carpobrotus* plots and the three most native treatments, with some degree of overlap between all treatments. Similarly, NMDS plots based on pan trap data from June (Fig. 11) show that

arthropod communities in high *Carpobrotus* and 1/3 native plots were different from those in 2/3 and 3/3 native plots which, in turn, were different from those in intact native plots. These differences are corroborated by MRPP analyses on all treatment pairs for each month and sampling technique (A's = 0.09 to 0.15, p's ≤ 0.001). Axis 1, which was associated with most of the treatment differences, explains between 39 to 69% of the variation for the 2013 analyses. Plant variables most strongly correlated with Axis 1 are %*Carpobrotus* cover and litter depth on one side, and overall plant H' diversity/native H' diversity on the other side.

Relationships between component taxa and NMDS axis 1 scores in 2013, which clearly distinguished between plots dominated by *Carpobrotus* versus plots dominated by native plants, suggest that among soil taxa, Formicidae and *Coelus ciliatus* (Tenebrionidae) were again associated with plots dominated by natives, joined by Melyridae and booklice (Trogiidae: detritivores), while silverfish (Lepismatidae: detritivores), click beetle larvae (Elateridae: predators), centipedes (Chilopoda: predators), fungus gnats (Sciaridae: detritivores), ground beetles (Carabidae: predators), and plant bugs (Miridae: herbivores) were associated with plots dominated by *Carpobrotus*. In March pan trap samples, Sciaridae, flower flies (Syrphidae: pollinators), Thripidae, long-legged flies (Dolichopodidae: predators), phorid flies (Phoridae: detritivores), stiletto flies (Therevidae: detritivores), plant lice (Psyllidae: herbivores), Bethylidae (parasitoids), big-headed flies (Pipunculidae: parasites), and leaf miner flies (Agromyzidae: herbivores) were most associated with *Carpobrotus*-dominated plots while Aphididae preferred native plant plots. Lastly, in June

pan trap samples Agromyzidae, Formicidae and sweat bees (Halictidae: pollinators) were positively, and Melyridae were negatively, related to *Carpobrotus* cover. Indicator species analysis revealed that the following taxa correlated with axes were also Indicator Species: Formicidae were indicators of 3/3 native plots in soil, in pan traps Sciaridae and Therevidae were indicators of high *Carpobrotus* plots in March, dance flies (Empidiidae: predators) were indicators of 1/3 native plant plots, Melyridae were indicators of 2/3 native plots, and lady bird beetles (Coccinellidae: predators) were indicators of intact native plots in June. Phoridae were indicators of 1/3 native plant plots in both months in pan traps. In addition, significant herbivorous indicator species for intact plots that were not well correlated with either axis were the leafhoppers (Cicadellidae: both months) and the fruit flies (Tephritidae: June) (all p's < 0.05).

Discussion

The abundance of a plant invader has long been suspected to influence its impact; however few studies have tested this relationship. Early conceptual models assumed that the relationship between abundance and impact is linear, with per-capita effects constant across the range of invader cover (Parker et al. 1999). However, I found a dramatic decline in arthropods in association with *Carpobrotus edulis* for the majority of taxa and guilds evaluated, with the slope steepest between zero and 30% *Carpobrotus* cover. These results indicate strong per capita effects at low invader abundances; this interaction between

invader cover and per-capita effects is consistent with recent conceptual models of invader impact (e.g., Lockwood et al. 2007).

Arthropod abundance consistently increased with plant H' diversity, but the relationship was typically linear rather than exponential, and its strength was never as great as for *Carpobrotus* cover. Therefore, while a reduction in plant diversity appears to be an important component of the effects of *Carpobrotus* on arthropod abundance, other factors must be contributing to the dramatic decline observed. Responses by individual feeding guilds and indeed particular taxa can help to explain the patterns found.

Soil detritivore abundance decreased then increased slightly with increasing *Carpobrotus* cover, and decreased with increasing litter depth, in both months. This appears to be due to preferences for native resources by some taxa, and for *Carpobrotus* by others, with both benefitting from more of their preferred resource. Of the soil detritivores, Tenebrionidae were most strongly and consistently associated with native-dominated dunes; these were primarily the larvae and adults of the fossorial dune beetle, *Coelus ciliatus*. Similarly, Snover (1992) reported that *Coelus globosus* adults and larvae were less abundant on *Carpobrotus* than on the native *Ambrosia* and exotic *Cakile* and that the diversity of fossorial insects as a whole declined with *Carpobrotus* invasion. Slobodchikoff and Doyen (1977) reported that the invasive perennial beach grass *Ammophila arenaria*, which also stabilizes California dune sand, exponentially decreased arthropod (particularly *Coelus*) abundances to near zero.

Carpobrotus has a dense, fibrous root system which stabilizes the upper meter of soil, reducing sand movement and changing the below-ground environment for soil dwelling invertebrates (D'Antonio and Mahall 1991; Snover 1992; Albert 2000; Molinari et al. 2007). Fossorial arthropods may be less abundant in areas where *Carpobrotus* dominates because their movement is inhibited by these dense roots, or because they avoid novel plants (Behavioral Constraint Hypothesis; Lankau et al. 2004). I have found in this study as well as a similar study at three other coastal dune sites (Chapter 2) that along with *Coelus ciliatus*, two other fossorial arthropod taxa were associated with native-dominated plots: flower beetles (*Notoxus*: Anthicidae), and dune spiders (*Lutica*: Zodariidae). All of these taxa scavenge beneath the surface in mobile sand environments (Doyen 1976; Zedler et al. 1992; Ramirez 1995). I have observed *Carpobrotus* roots extending beyond the above-ground canopy, and thus it may be that below-ground space is affected beyond what is visible above-ground. This could account for the exponential decline in soil arthropod abundance observed here.

Similar to overall soil arthropod abundance and soil detritivores, soil predator abundance declined exponentially between zero and 40-50% *Carpobrotus* cover. This was primarily due to a negative response by various members of the Formicidae (*Crematogaster*, *Monomorium*, and *Solenopsis*), which are all partially predators, as well as *Lutica*, discussed above. The negative response by native ants to *Carpobrotus* may be partially due to its facilitation of a different invader, the Argentine Ant (*Linepithema humile*). Only the Argentine ant was found in the *Carpobrotus*-dominated area prior to its

removal in 2010, while four native ant genera were found in the same area in 2013, largely in the plots where high native cover had been restored. A facilitative relationship could be due to increases in soil moisture, which has been tied to the ants' invasion success (Holway 1998; Menke et al. 2007). If Argentine ants keep out native ants as reported (Wetterer et al. 2001; Holway and Suarez 2006) then a decline in *Carpobrotus* cover due to removal followed by native plant restoration could have allowed native ants to return to the area.

In contrast to below-ground detritivores, above-ground detritivores (particularly flies in the families Sciaridae, Therevidae, and Phoridae) increased with increasing *Carpobrotus* cover and litter depth in June 2013. This is consistent with literature results showing positive associations between invertebrate detritivore abundance and litter levels (e.g., Gratton & Denno 2005; Kappes et al. 2007). I observed no relationship between aerial detritivore abundance and *Carpobrotus* cover or litter depth in March 2013, however. In 2010, flies in the families Heleomyzidae, Scathophagidae, and Anthomyiidae were abundant in *Carpobrotus* plots, apparently attracted to the 10-13 x greater litter levels found there than in intact, native plots. These detritivorous flies were largely responsible for the high arthropod abundance observed in *Carpobrotus* plots relative to native plots in 2010.

The exponential decrease in overall arthropod abundance observed in March pan traps is best explained by herbivores, which decreased with increasing *Carpobrotus* cover and increased with increasing plant diversity. This response was driven by Aphididae, which were strongly associated with native plots. In addition to Aphididae, which favored native

plots in 2010 as well, two other herbivore groups containing primarily specialists avoided *Carpobrotus* plots: Cicadellidae (March and June 2013), and Tephritidae (June 2013). Specialist herbivores are adapted to overcome a specific set of chemical and physical defenses displayed by their specific resource species, so tend to be less abundant than generalist herbivores on exotic plants (Schoonhoven 1972; Mattson 1980; Novotny et al. 2003; Carvalheiro et al. 2010; Almeida-Neto et al. 2011). The phylogenetic distance from an introduced plant species to the nearest native relative (taxonomic isolation) can predict the degree to which native herbivores will use the invader (Strong et al. 1984; Harvey et al. 2012). Because the genus *Carpobrotus* is relatively isolated taxonomically from the native flora of California (Hickman 1993), the negative effect of *Carpobrotus* on native specialist herbivores was expected.

Unexpectedly, however, two predominantly specialist herbivore groups favored *Carpobrotus*-dominated plots: Psyllidae (in March), and Agromyzidae (in both months). *Carpobrotus* has been on the central coast of California for over 100 years, and it seems that a number of herbivores have successfully colonized it. This includes Thripidae, which strongly favored *Carpobrotus* across all sampling periods, consistent with results reported in the literature (Vila et al. 1998).

Omnivores, parasitoids, and, to some extent, predators appear to be the source of an overall negative linear relationship observed between increasing *Carpobrotus* cover and arthropod abundance in June 2013. Omnivores, overwhelmingly dominated by flower beetles in the family Melyridae (Dasytinae), showed a strong negative response to

Carpobrotus invasion and a positive response to plant diversity in June, when they were most abundant, but not in March. They also preferred native plots in 2010. Dasytine melyrids frequent flowers and often feed on nectar and pollen; they may be more host-specialized than generally appreciated (Mawdsley 2003). Yet overall floral resources were likely more abundant in plots with *Carpobrotus* due to its prolific pollen production (Blake 1969). Hence our results may indicate a preference for native over *Carpobrotus* flowers by Dasytines, perhaps due to chemical or nutritional differences.

Parasitoid abundance was strongly, positively related to plant diversity and negatively related to *Carpobrotus* cover in June (but not in March). Parasitoids reached up to 5x higher abundance in June than in March; the greater response in June may be due simply to the fact that more had emerged from their hosts at this time. They were likely responding to herbivore abundance, which was strongly and negatively affected in March, and positively related to plant diversity.

Predators trapped in pans exhibited a u-shaped relationship with *Carpobrotus* cover in June, perhaps in response to prey, some of which decreased with *Carpobrotus* (omnivores, parasitoids), and some of which increased (detritivores and Thripidae). The predators most associated with plots dominated by native plant species were beetles in the family Coccinellidae, which were likely responding to the greater abundance of their aphid prey. Those that preferred *Carpobrotus* included two families of spiders (Lycosidae and Salticidae), which are known to be generalist predators. Pan-trapped predators did not show a significant response to *Carpobrotus* cover in March, perhaps due to fewer

significant responses in that month by potential prey. They also did not have a significant relationship in either month with plant diversity, a variable which is perhaps too far removed from, and thus less important than, prey abundance.

Contrary to predictions, pollinator abundance was not related to *Carpobrotus* cover in either month. In three other coastal California dunes, I have found both positive and negative responses by pollinators to *Carpobrotus* cover. In other systems, the presence of *Carpobrotus* has been found to increase pollinator visitation to native plant species more often than it reduces it (Moragues and Traveset 2005; Bartomeus et al. 2008). *Carpobrotus edulis* has relatively high densities of large, conspicuous flowers that bloom during long periods of the year (Table 1), which typically benefits pollinators (Bjerknes et al. 2007, Morales and Traveset 2009). There was a trend for pollinator abundance to be positively associated with plant diversity in March. More investigation is needed on the specialization level of pollinators; those associated with *Carpobrotus* in this study included the Halictidae (primarily *Lasioglossum*), which are predominantly generalists (Dr. Robbin Thorp, personal communication). Further, *Apis mellifera* and *Bombus* sp., also generalists, were observed utilizing *Carpobrotus*, but were only rarely captured in pan traps.

Above- vs. below-ground residence and season were both important in determining arthropod responses to *Carpobrotus* invasion. Responses were generally stronger among soil arthropods than pan-trapped arthropods, perhaps due to structural changes in the below-ground environment. Further, responses were stronger in June compared to March. This may be due to a higher abundance overall in June (Table 1), as well as a greater

abundance and diversity of taxa such as leafhoppers (Cicadellidae), and parasitoids, which had not yet emerged in great numbers in March.

Across sampling techniques and times I found a general change in arthropod composition between *Carpobrotus* control plots and 1/3 native plots vs. 2/3 native, 3/3 native, and Intact (remnant native) plots, driven by *Carpobrotus* cover in the former two treatments (*Carpobrotus* dominating) and H' diversity in the latter three treatments. The soil and March pan trap data indicated that arthropod communities converged to natural configurations within a few years after *Carpobrotus* was removed and replaced with native vegetation, while the June pan trap data indicated that there were still differences between restored and natural areas.

Conclusion

This study evaluated the response of arthropod assemblages to multiple manipulated levels of an invader and native plant species. It demonstrates that *Carpobrotus* invasion causes a significant reduction in arthropod abundance and richness, a substantial change in feeding guild structure, and altered abundances of component taxa, and that it does so at rather low levels of abundance: impact are significant even before the invader's cover reaches 50%. This has direct negative implications for wildlife that prey on arthropods, including birds, herpetofauna, and small mammals, as well as the

ecosystem functions that they are performing (van Riper et al. 2008; Gullan and Cranston 2005).

Quantitative knowledge of relationships between invader abundance and impact will enable policy makers and land managers to set targets and prioritize management practices (Byers et al. 2002; Andreu et al. 2009). Furthermore, determination of the magnitude and patterns of invasive plant impacts on arthropod abundance, diversity, and structure may guide efforts to restore native diversity and ecosystem functions, e.g., by helping to determine appropriate levels of invasive plant control and native plant establishment (Le Maitre et al. 2011). In a more general sense, this study will provide data on the effects of invasive species on native communities, adding to the worldwide database on native biodiversity responses to rapidly changing environments (Hillebrand et al. 2008).

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Table 1. Vegetation characteristics of the treatments and controls used, March 2013.

	Treatment				
	Carpobrotus	1/3 native	2/3 native	3/3 native	Intact
n	7	6	6	7	7
% *Carpobrotus* cover	68 (3.6) A	54 (6.6) B	23 (3.9) C	9 (2.6) D	0 (0) D
% Native cover	3.0 (3.0) A	4.3 (3.2) A B	12.8 (3.2) B C	14.3 (3.0) C	28.1 (3.0) D
Plant H' diversity	0.20 (0.17) A	0.43 (0.19) A	0.42 (0.19) B	1.14 (0.17) B	1.28 (0.17) B
Native plant H' diversity	0.13 (0.1) A	0.23 (0.1) A B	0.69 (0.2) B	0.82 (0.2) C	1.13 (0.1) C
Species richness	3.1 (1.3) A	12.0 (1.4) B	13.8 (1.4) BC	17.1 (1.3) C	7.7 (1.3) D
% points with *Carpobrotus* flowers	25.7 (8.7) A	22.0 (9.1) A	11.8 (4.9) AB	1.7 (1.1) BC	0 (0) C
% points with non-*Carpobrotus* flowers	0 (0) A	3.5 (3.1) A	9.2 (5.6) A	12.4 (6.6) A	2.0 (0.9) A
Average height	10.5 (1.6) A	10.7 (1.7) A	10.8 (1.7) A	13.3 (1.6) A	19.3 (1.6) B
Coefficient of height variation	0.69 (0.09) A	0.45 (0.03) A	0.61 (0.05) A	0.67 (0.10) A	0.55 (0.12) A
% Dead cover	2.3 (1.1) A	4.2 (1.9) AB	6.3 (1.0) AB	4.3 (1.0) B	40.6 (4.1) C
Average litter depth	13.7 (0.9) A	10.2 (1.0) B	4.4 (1.0) C	0.9 (0.9) D	1.3 (0.9) D

Note: n is the number of plots in each category; numbers in the body of the table are mean values and numbers in parentheses are SEs. Capital letters below each row indicate statistically significant differences among treatments based on ANOVAs and t-tests or Wilcoxon rank sums tests (% flowers) to compare each pair, with comparisonwise corrections using FDR ($\alpha = 0.05$, values with the same letter are not significantly different). Data for % dead cover were log (x + 1) transformed to meet test assumptions.

Table 2. Soil characteristics of high *Carpobrotus* vs. intact native plots.

	Treatment	
	Carpobrotus	Intact
% Soil moisture	0.43	0.06
(July 2011)**	(0.13)	(0.01)
	A	B
Average litter depth (cm)	13.7	1.3
(March 2013)	(0.9)	(0.9)
	A	B
Litter biomass (g/L)	870.4	68.0
(March 2012)***	(68.2)	(73.7)
	A	B
% Sand	94.1	96.4
(July 2011) ‡	(1.1)	(0. 7)
	A	A
pH	6.0	6.2
(May 2010)	(0.2)	(0.1)
	A	A
Conductivity	45	30
(microsiemens/cm)	(7)	(3)
(May 2010)*	A	B

Note: numbers in the body of the table are mean values and numbers in parentheses are SEs. Conductivity values were log- transformed to meet test assumptions. Significance (Student's t-test) is indicated as follows: ‡ $0.1 > P \geq 0.05$, * $0.05 > P \geq 0.01$, ** $0.01 > P \geq 0.001$, *** $P < 0.0001$

Table 3. Relationships (all linear) between arthropod feeding guild abundances and selected vegetation variables, 2013.

Variable	Variable	r^2	β	t	p
Detritivores, March soil ‡	Litter depth	0.10	-0.04	-1.88	0.07
Detritivores, June soil**	Litter depth	0.31	-0.26	-3.64	0.001
Detritivores, March pan traps	Litter depth	0.03	0.13	0.97	0.34
Detritivores, June pan traps**	Litter depth	0.30	0.05	3.60	0.001
Herbivores, March pan traps***	Plant H' diversity	0.37	0.74	4.30	0.0002
Herbivores, June pan traps**	Plant H' diversity	0.20	-0.51	-2.78	0.009
Herbivores June pan traps (thrips excluded)	Plant H' diversity	0.01	-0.10	-0.67	0.50
Omnivores, March pan traps	Plant H' diversity	0.07	0.40	1.53	0.14
Omnivores, June pan traps**	Plant H' diversity	0.22	0.77	2.95	0.006
Parasitoids, March pan traps	Plant H' diversity	0.00	-0.10	-0.14	0.89
Parasitoids, June pan traps***	Plant H' diversity	0.31	0.68	3.67	0.0009
Pollinators, March pan traps ‡	Plant H' diversity	0.33	0.09	1.72	0.10
Pollinators, June pan traps	Plant H' diversity	0.02	0.21	0.75	0.46
Predators, March soil***	Plant H' diversity	0.36	0.94	4.18	0.0002
Predators, June soil ‡	Plant H' diversity	0.52	0.11	1.94	0.06
Predators, March pan traps	Plant H' diversity	0.05	-0.21	-1.28	0.21

Predators, June pan traps	Plant H' diversity	0.04	0.16	-1.08	0.29

All arthropod variables were log (x + 1) transformed before analysis except for litter depth.MDegrees of freedom (model, error) = 3, 27 for June soil, 3, 28 for June pan traps, 3, 29 for March soil and pan traps. Significance: ‡ 0.1 > P ≥ 0.05, * 0.05 > P ≥ 0.01, ** 0.01 > P ≥ 0.001, *** P < 0.001.

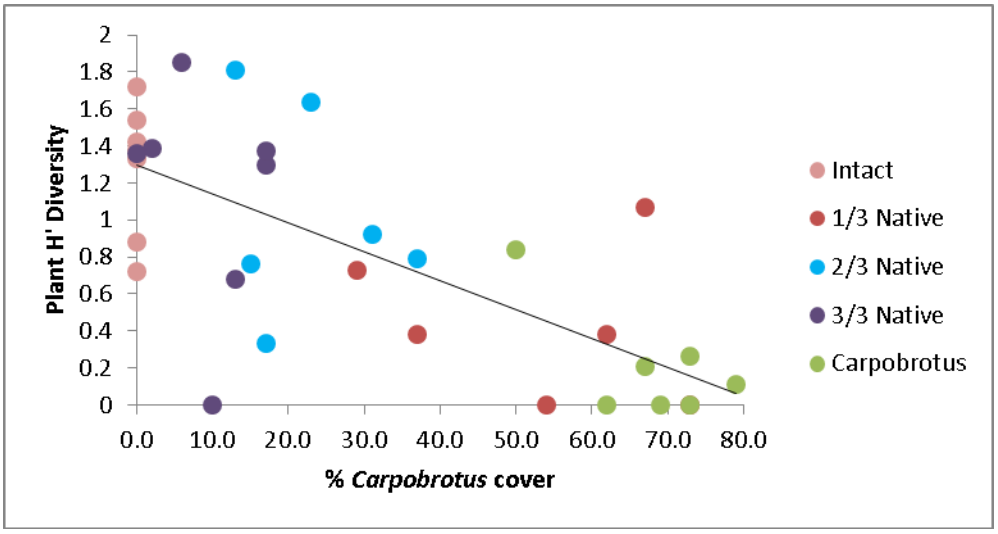

Figure 1. Relationship of *Carpobrotus* cover and plant H' diversity across plots in 2013, illustrating the gradient of these variables that was created by experimental manipulations. H' Div = 1.30 - 0.02*%CAED; Rsquare = 0.52, t= -5.8, p<0.0001.

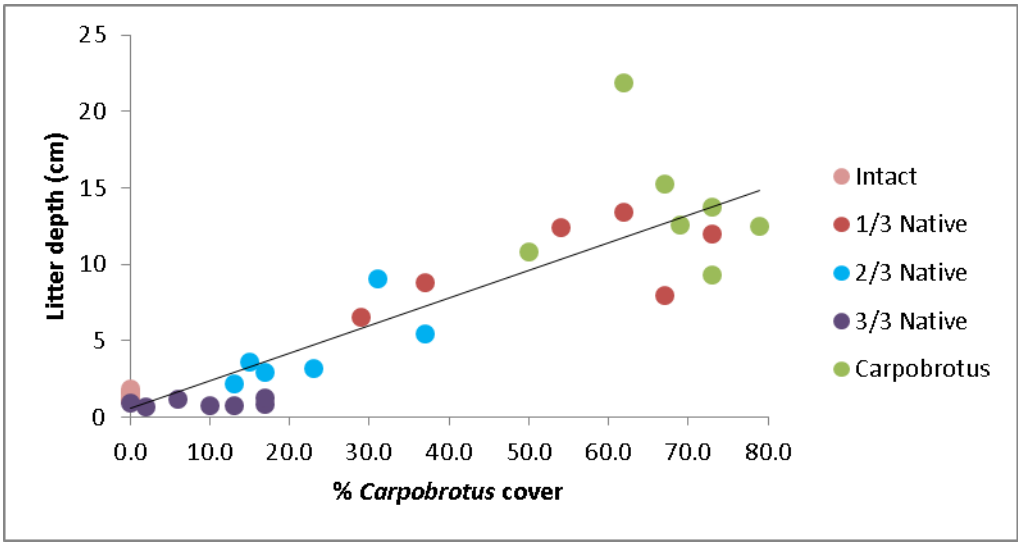

Figure 2. Relationship of *Carpobrotus* cover and litter depth across plots in 2013. AvgLitDepth = 0.53 + 0.19*%CAED; Rsquare = 0.82, t= 11.8, p<0.0001.

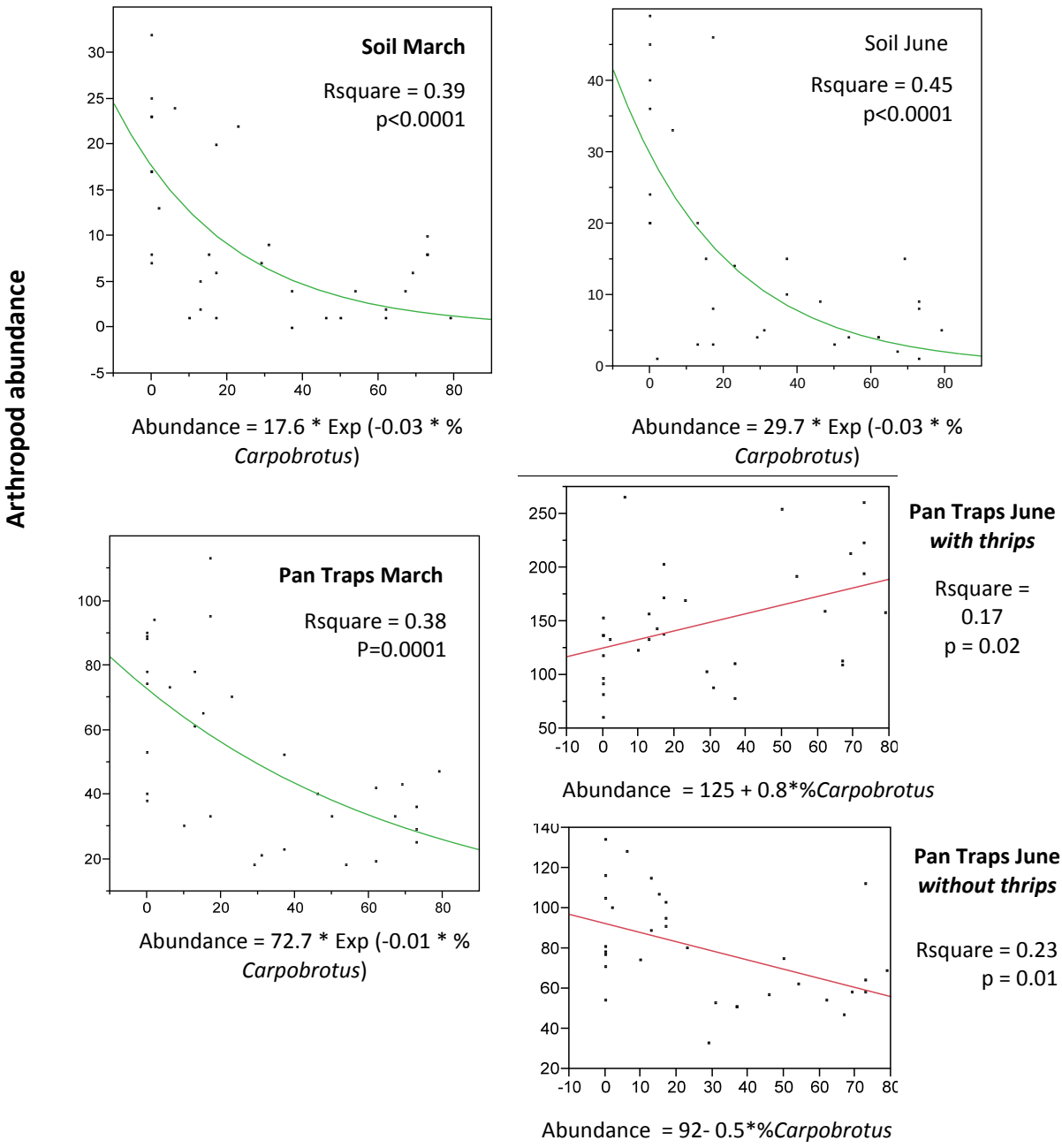

Figure 3. Relationships between overall arthropod abundance and *Carpobrotus* cover for soil (top) and pan trap (bottom) samples in March (left) and June (right) 2013. Regression equations and associated R^2 and p values are shown.

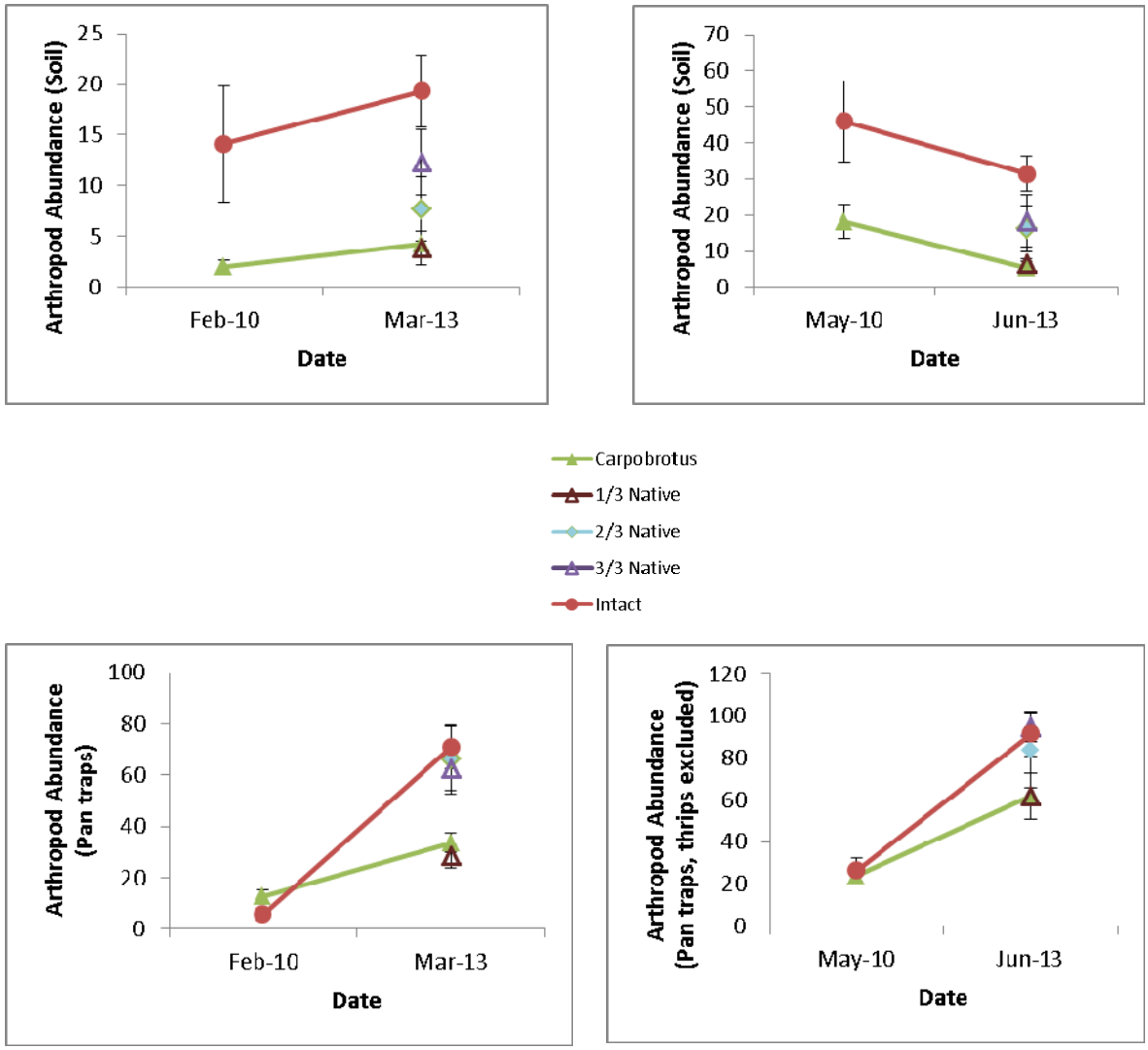

Figure 4. Arthropod abundance, late winter/early spring (left) and late spring/early summer (right), for soil samples (top) and pan traps (bottom), prior to revegetation (2010) and following revegetation (2013). All 2010 differences are all significant at the p=0.05 level except for May pan traps. The following differences were significant in 2013: Intact vs. *Carpobrotus* control, 1/3, and 2/3 in March soil; Intact vs. *Carpobrotus* control and 1/3 native in June soil; *Carpobrotus* control vs. Intact, and 1/3 native vs. Intact, 3/3 native, and 2/3 native in March pan traps; none in June pan traps.

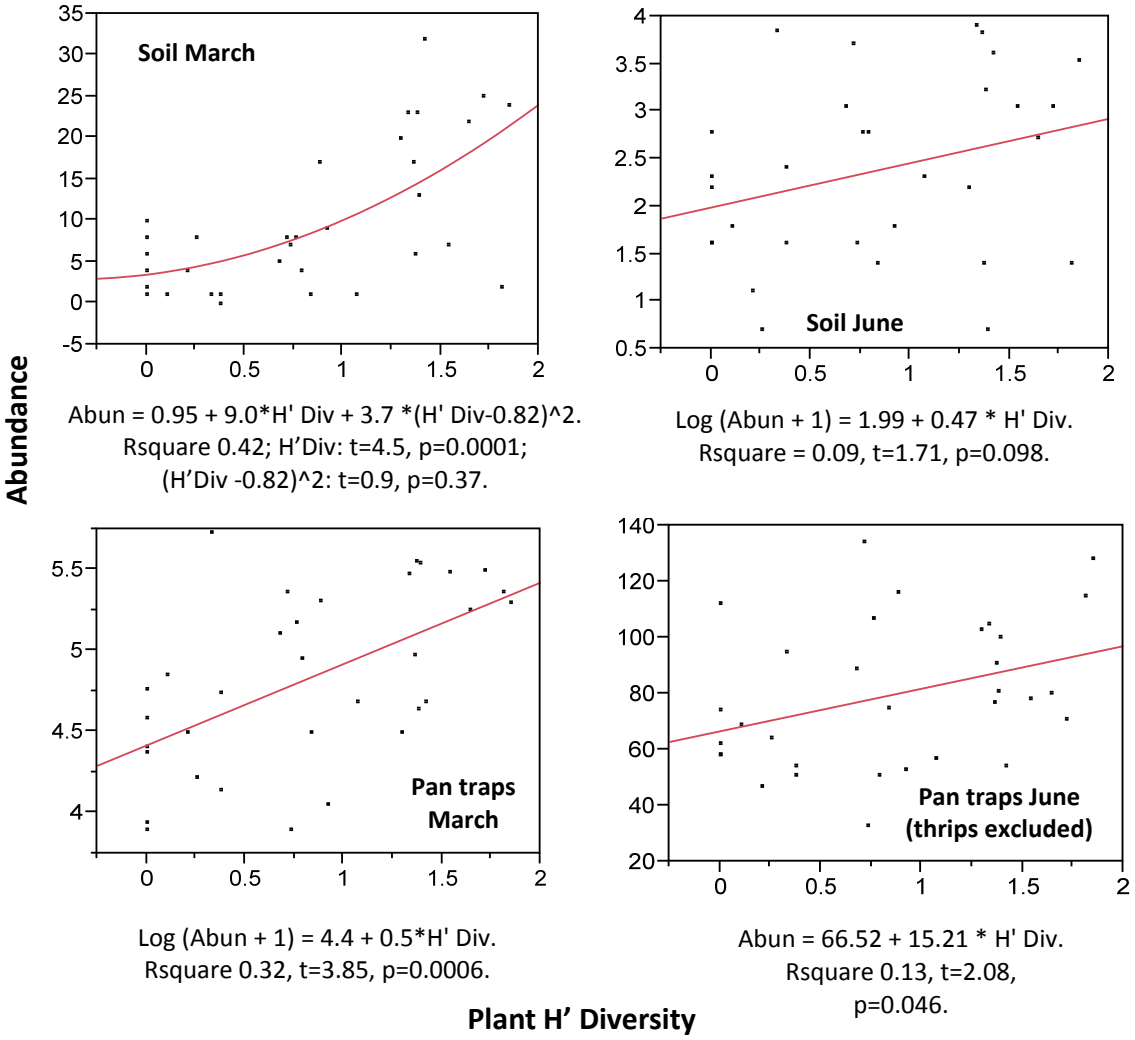

Figure 5. Relationships between overall arthropod abundance and plant H' diversity for soil (top) and pan trap (bottom) samples in March (left) and June (right) 2013. Regression equations and associated R^2 and p values are shown.

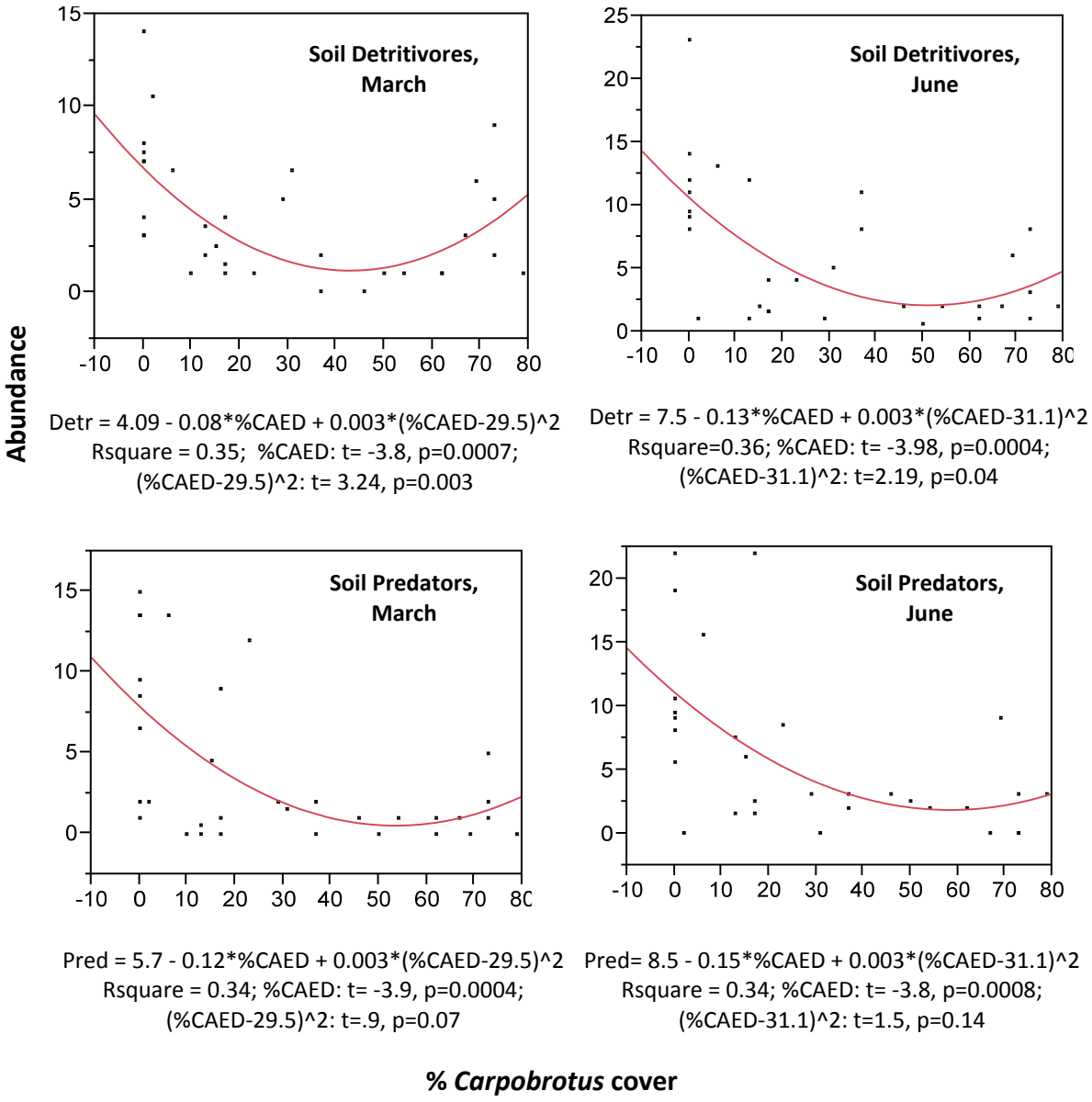

Figure 6. Relationships between arthropod feeding guild abundance and *Carpobrotus* cover for soil detritivores (top) and soil predators (bottom) samples in March (left) and June (right) 2013. Regression equations and associated R^2 and p values are shown.

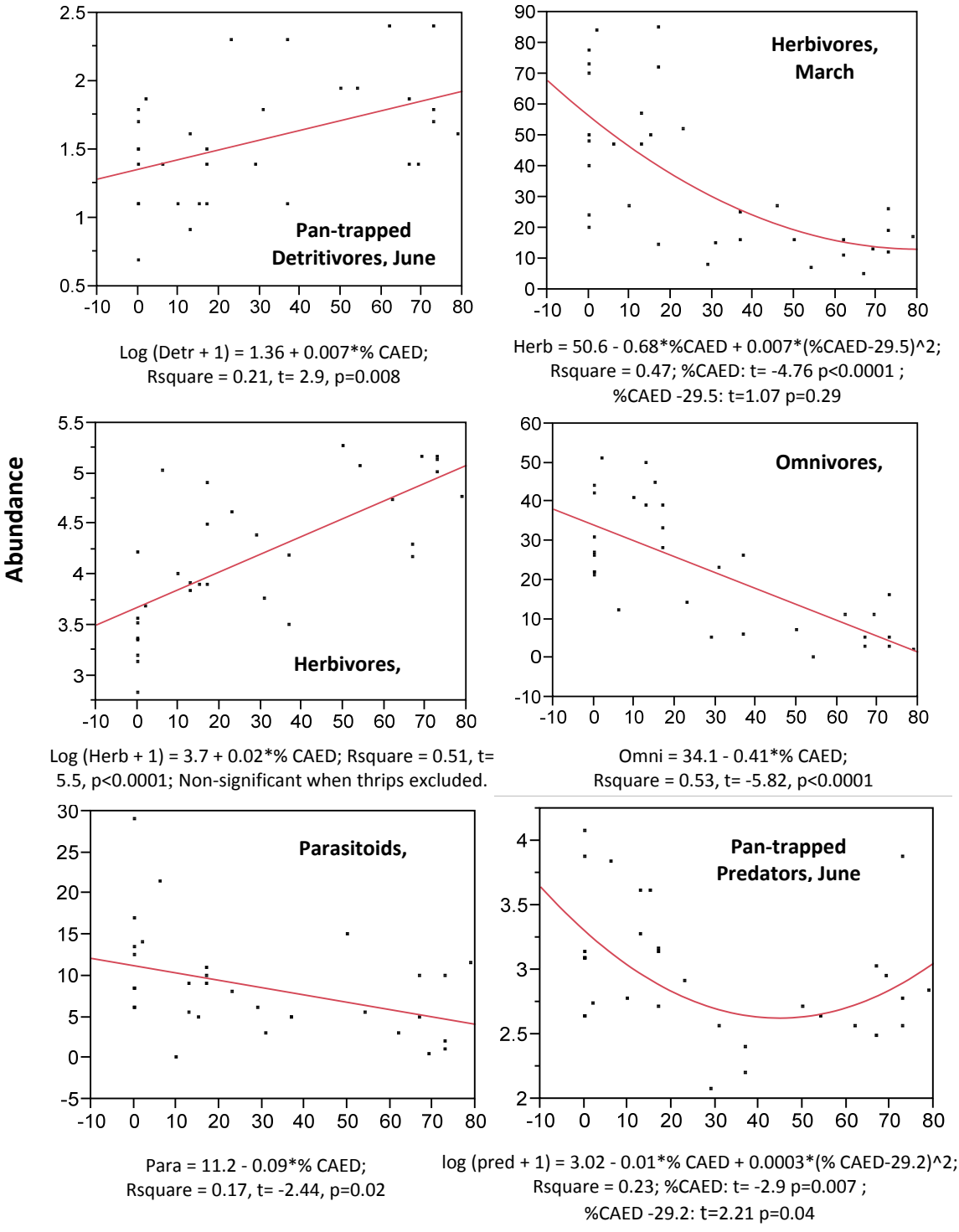

Figure 7. Significant relationships between arthropod feeding guild abundance and *Carpobrotus* cover for feeding guilds in pan traps, March and June 2013. Regression equations and associated R^2 and p values are shown.

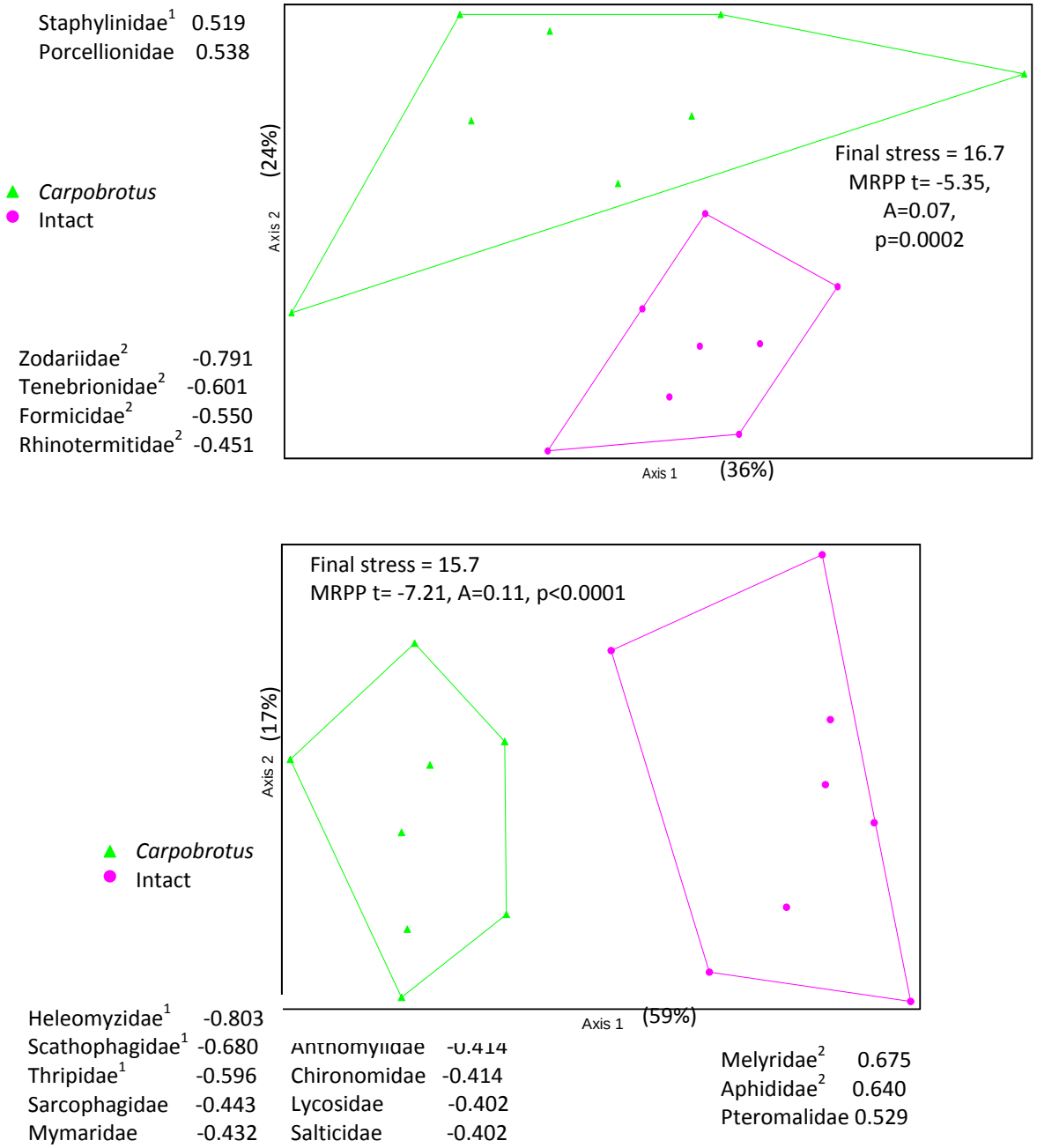

Figure 8. Results of a nonmetric multidimensional scaling (NMDS) analysis applied to the matrix of the relative abundances of all arthropod families by treatment in February and May 2010 soil samples combined, above, and February and May 2010 pan traps combined, below. Taxa most correlated (r ≥0.4) with each NMDS axis and their Pearson's correlation coefficients are noted in the margins of the diagram; superscript numbers represent Indicator Species for *Carpobrotus* (1) or Intact (2) plots.

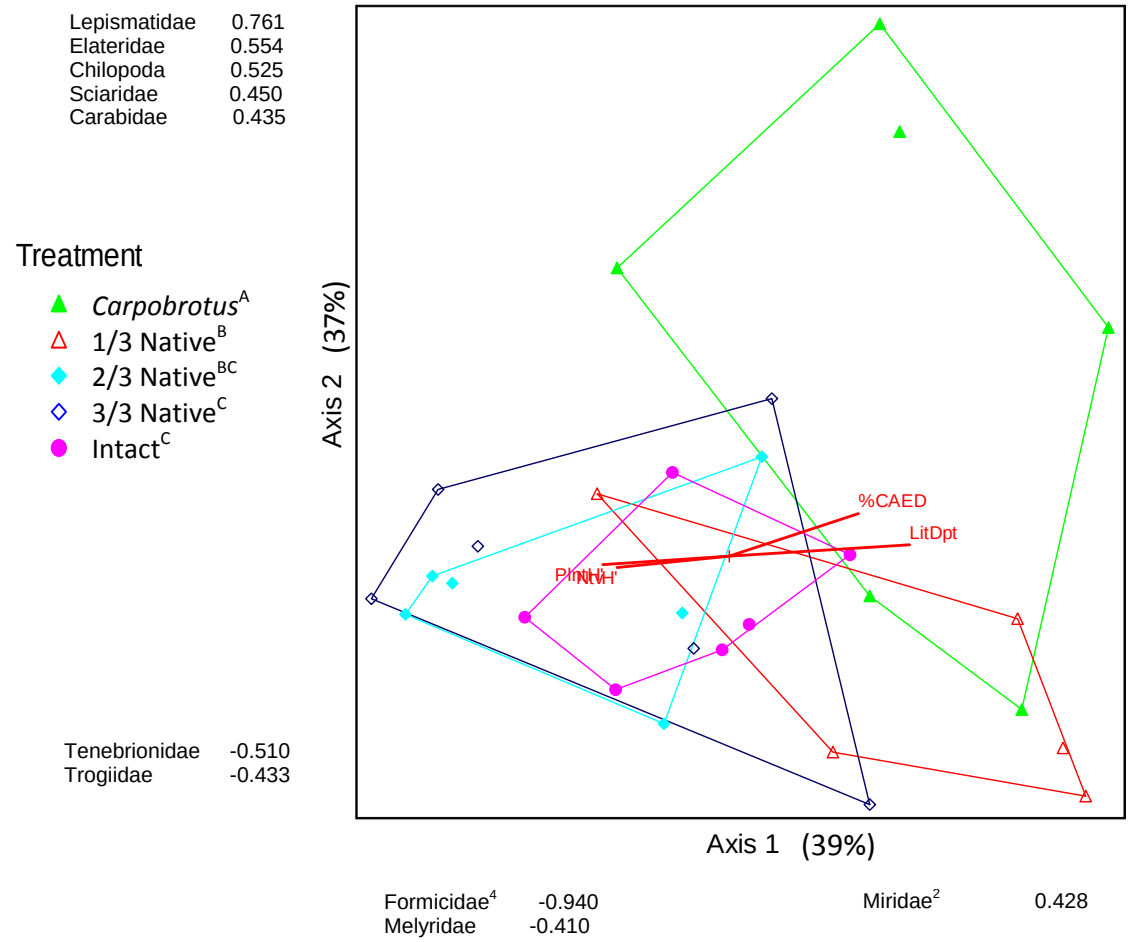

Figure 9. Results of a nonmetric multidimensional scaling (NMDS) analysis applied to the matrix of the relative abundances of all insect families and arthropod orders in March and June 2013 soil samples combined, by treatment. For the NMDS 3-dimensional solution, final stress = 9.6. Taxa most correlated (r ≥0.4) with each NMDS axis and their Pearson's correlation coefficients are noted in the margins of the diagram; superscript numbers represent Indicator Species for *Carpobrotus* control plots (1), 1/3 native (2), 2/3 native (3), 3/3 native (4), and Intact plots (5). Lines indicate the vegetation variables most associated with the NMDS axes (r ≥0.4): *Carpobrotus edulis* cover (CAED) and native plant H' diversity. MRPP t= -7.0, A=0.15, p<0.0001. Superscript letters on treatment groups indicate significant differences per MRPP and post-correction with FDR.

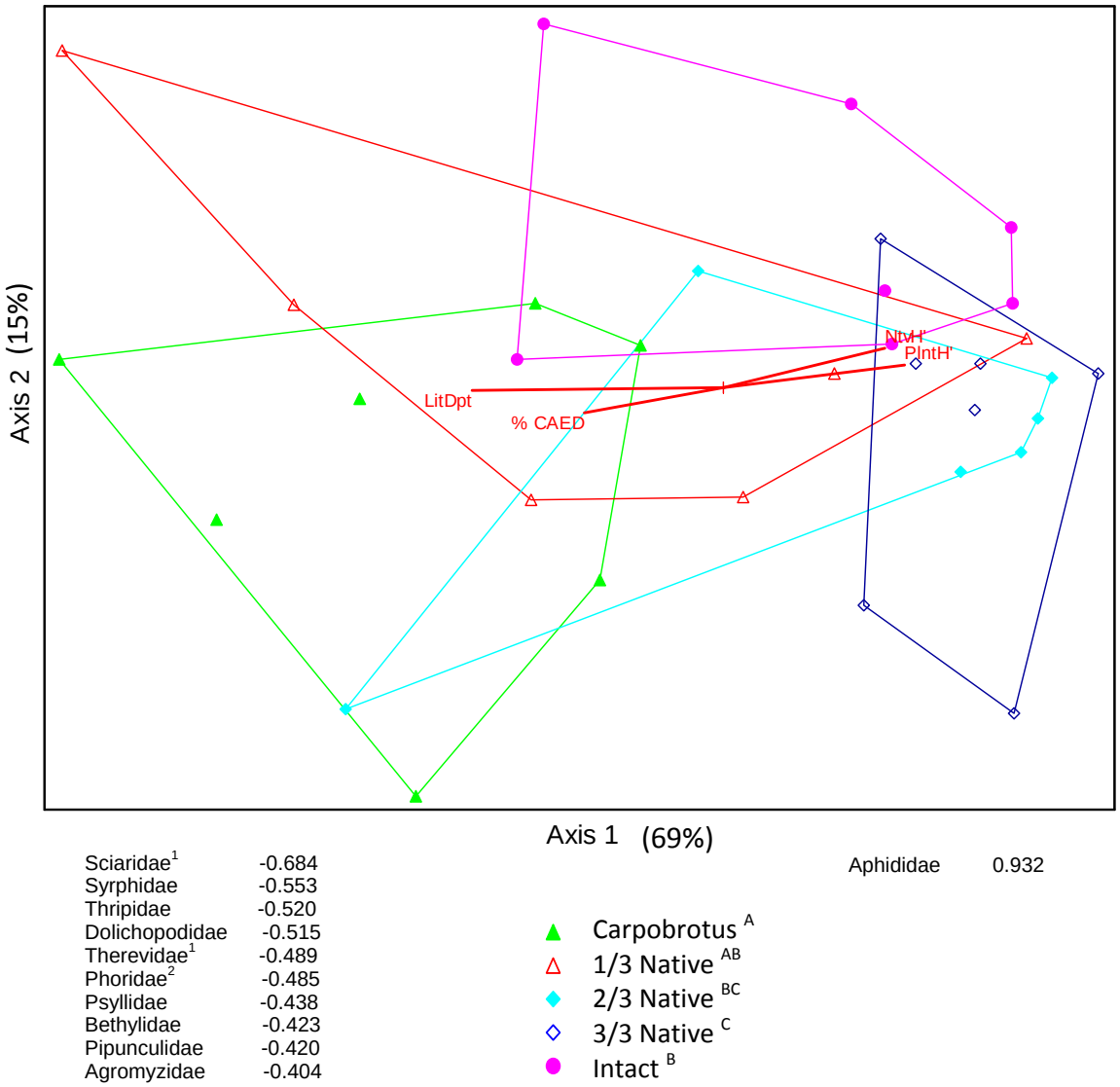

Figure 10. Results of a nonmetric multidimensional scaling (NMDS) analysis applied to the matrix of the relative abundances of all insect families and arthropod orders in March 2013 pan traps by treatment. For the NMDS 2-dimensional solution, final stress = 16.0. Taxa most correlated (r ≥0.4) with each NMDS axis and their Pearson's correlation coefficients are noted in the margins of the diagram; superscript numbers represent Indicator Species for *Carpobrotus* control plots (1), 1/3 native (2), 2/3 native (3), 3/3 native (4), and Intact plots (5). Lines indicate the vegetation variables most associated with the axes (r ≥0.4): *Carpobrotus edulis* cover (% CAED), litter depth (LittDpth), plant H' diversity (PlntH'), and native plant H' diversity (NtvH'). MRPP t= -4.3, A=0.09, p=0.001. Superscripts on treatment groups indicate significant differences per MRPP and post-correction with FDR. Superscripts on treatment groups indicate significant differences per MRPP and post-correction with FDR.

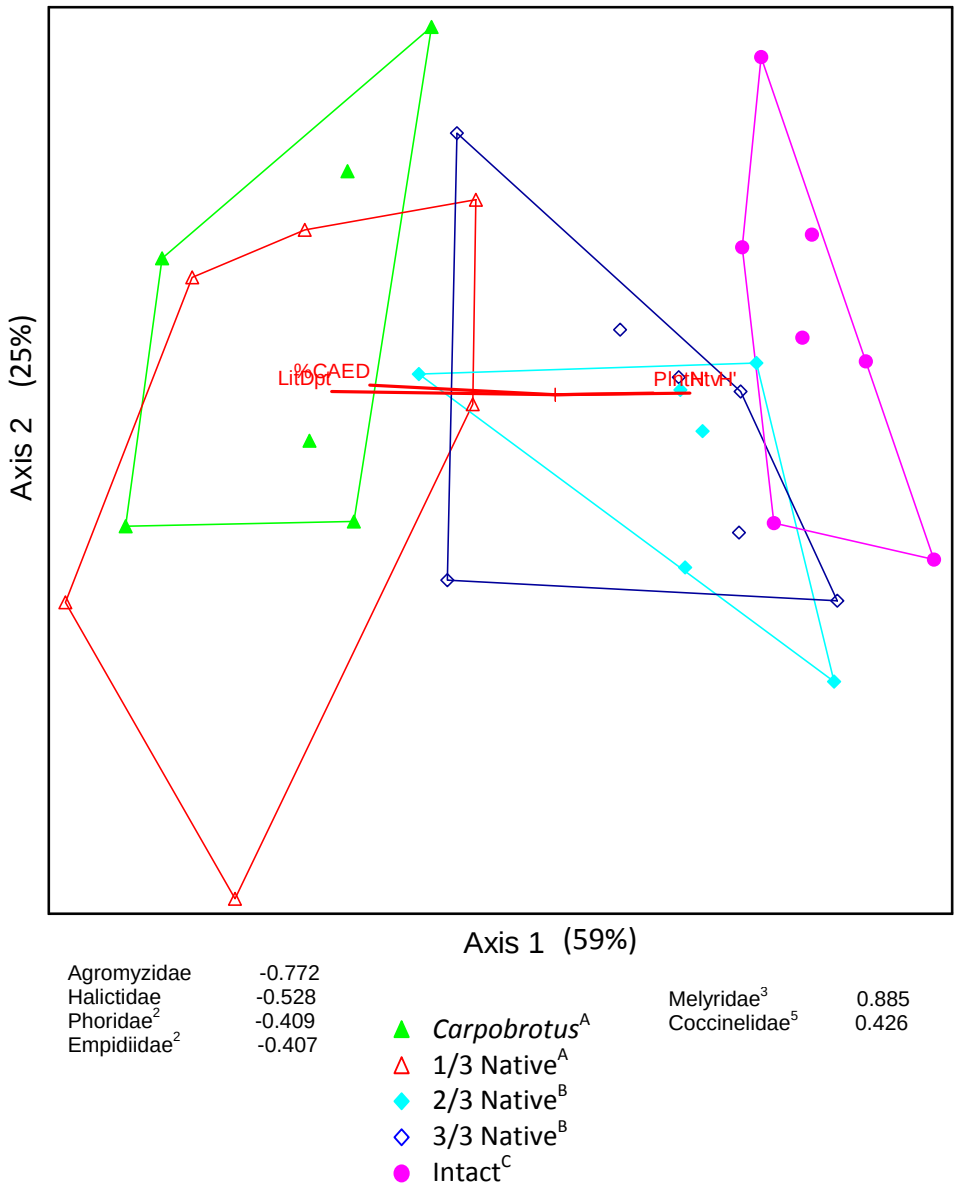

Figure 11. Results of a nonmetric multidimensional scaling (NMDS) analysis applied to the matrix of the relative abundances of all insect families and arthropod orders in June 2013 pan traps across plots. Thrips, which in the initial analysis were 99% correlated with *Carpobrotus*, were excluded from this analysis. For the NMDS 3-dimensional solution, final stress = 9.7. Taxa correlated (r ≥0.4) with each NMDS axis and their Pearson's correlation coefficients are noted in the margins of the diagram; superscript numbers represent Indicator Species for *Carpobrotus* control plots (1), 1/3 native (2), 2/3 native (3), 3/3 native (4), and Intact plots (5). Lines indicate the vegetation variables most associated with the NMDS axes (r ≥0.4): *Carpobrotus edulis* cover (CAED) litter depth (LitDpt), and native plant H' diversity (PlntNtv H'). MRPP t= -7.0, A=0.15, p<0.0001. Superscripts on treatment groups indicate significant differences per MRPP and post-correction with FDR.

Supplemental Information, Chapter 3

Table S1. Arthropod taxa collected from plots at Coal Oil Point Reserve, California, in 2013, including taxonomic classification, collection in soil core or pan trap samples, and feeding group designations. Adults unless otherwise indicated.

Class/Subclass	Order	Family	Soil	Pan	Feeding Group
Arachnida	Araneae	Corinnidae: *Scotinella* sp.	X		predator
Arachnida	Araneae	Dictynidae: *Dictyna aggressa*	X		predator
Arachnida	Araneae	Gnaphosidae: *Zelotes nilicola*	X		predator
Arachnida	Araneae	Linyphiidae: *Erigone dentosa*	X		predator
Arachnida	Araneae	Lycosidae *Pardosa ramulosa*		X	predator
Arachnida	Araneae	Mygalomorpha unknown (imm)	X		predator
Arachnida	Araneae	Oonopidae: *Orchestina moaba*	X		predator
Arachnida	Araneae	Salticidae unknown (imm)	X		predator
Arachnida	Araneae	Theridiidae: *Crustulina sticta*	X		predator
Arachnida	Araneae	Zodariidae: *Lutica* sp.	X	X	predator
Chilopoda	Geophilomorpha	Unknown	X		predator
Chilopoda	Lithobiomorpha	Unknown	X		predator
Diplopoda	Spirostreptida	Unknown	X		detritivore
Insecta	Coleoptera	Anobiidae		X	detritivore
Insecta	Coleoptera	Anthicidae	X	X	detritivore
Insecta	Coleoptera	Anthribidae		X	herbivore
Insecta	Coleoptera	Brentidae	X		herbivore
Insecta	Coleoptera	Cantharidae	X		predator
Insecta	Coleoptera	Carabidae	X	X	predator
Insecta	Coleoptera	Chrysomelidae		X	herbivore
Insecta	Coleoptera	Coccinellidae: *Cycloneda sanguinea*	X		predator
Insecta	Coleoptera	Coccinellidae: *Hyperaspidius* sp.	X		predator
Insecta	Coleoptera	Curculionidae: *Trigonoscuta*	X	X	herbivore
Insecta	Coleoptera	Elateridae (larvae)	X		predator
Insecta	Coleoptera	Hydrophilidae		X	omnivore
Insecta	Coleoptera	Latridiidae: *Aridius* sp.	X		detritivore
Insecta	Coleoptera	Latridiidae: *Corticarina* sp.	X		detritivore
Insecta	Coleoptera	Latridiidae: *Melanophthalma* sp.	X		detritivore
Insecta	Coleoptera	Leiodidae: *Agathidium*	X		detritivore
Insecta	Coleoptera	Melyridae: Dasytinae spp.	X	X	omnivore

Insecta	Coleoptera	Mordellidae	X	X	herbivore
Insecta	Coleoptera	Ptiliidae	X		detritivore
Insecta	Coleoptera	Scarabaeidae: *Aegialia* sp.	X	X	detritivore
Insecta	Coleoptera	Scarabaeidae: *Dichelonyx* sp.	X		herbivore
Insecta	Coleoptera	Scarabaeidae: *Tesarius* sp.	X	X	detritivore
Insecta	Coleoptera	Staphylinidae: *Aleocharinae* sp.	X		predator
Insecta	Coleoptera	Staphylinidae: *Medon* sp.	X		predator
Insecta	Coleoptera	Staphylinidae: *Quedius* sp.	X		predator
Insecta	Coleoptera	Staphylinidae: *Sepedophilus* sp.	X		predator
Insecta	Coleoptera	Staphylinidae: *Tachyporus* sp.	X		predator
Insecta	Coleoptera	Tenebrionidae: *Coelus ciliatus*	X	X	detritivore
Insecta	Collembola	Entomobryidae		X	detritivore
Insecta	Collembola	Hypogastruridae		X	detritivore
Insecta	Collembola	Isotomidae		X	detritivore
Insecta	Collembola	Poduridae	X		detritivore
Insecta	Collembola	Sminthuridae		X	
Insecta	Diplura	Campodeidae	X		detritivore
Insecta	Diptera	Agromyzidae		X	herbivore
Insecta	Diptera	Anthomyiidae		X	detritivore
Insecta	Diptera	Anthomyzidae		X	detritivore
Insecta	Diptera	Asilidae		X	predator
Insecta	Diptera	Bibionidae	X		detritivore
Insecta	Diptera	Calliphoridae		X	nectarivore
Insecta	Diptera	Cecidomyiidae	X	X	detritivore
Insecta	Diptera	Ceratopogonidae		X	parasite
Insecta	Diptera	Chironomidae		X	non-feeding (adults)
Insecta	Diptera	Chloropidae (Oscinellinae)		X	detritivore
Insecta	Diptera	Conopidae		X	parasite
Insecta	Diptera	Culicidae		X	Ectoparasite/ nectar
Insecta	Diptera	Dolichopodidae		X	predator
Insecta	Diptera	Empidiidae		X	predator
Insecta	Diptera	Fanniidae		X	detritivore
Insecta	Diptera	Heleomyzidae		X	detritivore
Insecta	Diptera	Phoridae		X	detritivore
Insecta	Diptera	Pipunculidae		X	parasite
Insecta	Diptera	Platypezidae		X	detritivore
Insecta	Diptera	Sarcophagidae (non-Sarcophaga)		X	nectar
Insecta	Diptera	Sarcophagidae: Sarcophaga		X	detritivore
Insecta	Diptera	Scathophagidae		X	predator

Insecta	Diptera	Sciaridae	X	X	detritivore
Insecta	Diptera	Syrphidae		X	pollinator
Insecta	Diptera	Tachinidae		X	parasitoid, pollinator
Insecta	Diptera	Tephritidae		X	herbivore
Insecta	Diptera	Therevidae	X	X	detritivore
Insecta	Diptera	Tipulidae larva		X	detritivore
Insecta	Hemiptera	Anthocoridae	X	X	predator
Insecta	Hemiptera	Aphididae	X	X	herbivore
Insecta	Hemiptera	Aradidae	X		detritivore
Insecta	Hemiptera	Cercopidae		X	herbivore
Insecta	Hemiptera	Cicadellidae	X	X	herbivore
Insecta	Hemiptera	Coccoidea		X	herbivore
Insecta	Hemiptera	Delphacidae		X	herbivore
Insecta	Hemiptera	Coreidae		X	herbivore
Insecta	Hemiptera	Largidae	X		herbivore
Insecta	Hemiptera	Lygaeidae		X	herbivore
Insecta	Hemiptera	Miridae	X	X	herbivore
Insecta	Hemiptera	Psyllidae		X	herbivore
Insecta	Hemiptera	Saldidae		X	predator
Insecta	Hemiptera	Tingidae		X	herbivore
Insecta	Hymenoptera	Aphelinidae	X	X	parasitoid
Insecta	Hymenoptera	Apidae		X	pollinator
Insecta	Hymenoptera	Bethylidae	X	X	parasitoid
Insecta	Hymenoptera	Braconidae	X	X	parasitoid
Insecta	Hymenoptera	Ceraphronidae		X	parasitoid
Insecta	Hymenoptera	Chalcididae		X	parasitoid
Insecta	Hymenoptera	Chrysididae		X	parasitoid
Insecta	Hymenoptera	Colletidae		X	pollinator
Insecta	Hymenoptera	Cynipidae		X	parasitoid
Insecta	Hymenoptera	Dryinidae		X	parasitoid
Insecta	Hymenoptera	Encyrtidae		X	parasitoid
Insecta	Hymenoptera	Eulophidae		X	parasitoid
Insecta	Hymenoptera	Figitidae		X	parasitoid
Insecta	Hymenoptera	Formicidae: Crematogaster	X	X	detritivore, predator
Insecta	Hymenoptera	Formicidae: Linepithema	X	X	detritivore, predator
Insecta	Hymenoptera	Formicidae: Monomorium	X	X	detritivore, predator

Insecta	Hymenoptera	Formicidae: Solenopsis	X	X	herbivore, predator
Insecta	Hymenoptera	Formicidae: Tapinoma	X	X	detritivore
Insecta	Hymenoptera	Formicidae: Temnothorax	X	X	omnivore
Insecta	Hymenoptera	Halictidae		X	pollinator
Insecta	Hymenoptera	Ichneumonidae		X	parasitoid
Insecta	Hymenoptera	Megaspilidae	X		parasite
Insecta	Hymenoptera	Mymaridae		X	parasitoid
Insecta	Hymenoptera	Perilampidae		X	parasitoid
Insecta	Hymenoptera	Pompilidae		X	predator
Insecta	Hymenoptera	Pteromalidae		X	parasitoid
Insecta	Hymenoptera	Scelionidae		X	parasitoid
Insecta	Hymenoptera	Sphecidae		X	predator
Insecta	Hymenoptera	Torymidae		X	parasitoid
Insecta	Hymenoptera	Trichogrammatidae		X	parasitoid
Insecta	Hymenoptera	Vespidae		X	predator
Insecta	Isoptera	Rhinotermitidae	X		herbivore
Insecta	Lepidoptera	Gelechiidae		X	pollinator
Insecta	Lepidoptera	Geometridae larva		X	herbivore
Insecta	Lepidoptera	Heleodinidae		X	pollinator
Insecta	Lepidoptera	Sphingidae larva		X	herbivore
Insecta	Microcoryphia	Machilidae	X	X	
Insecta	Microcoryphia	Meinertellidae	X		detritivore
Insecta	Neuroptera	Myrmeliontidae larva	X		predator
Insecta	Orthoptera	Acrididae		X	herbivore
Insecta	Psocoptera	Psocidae	X	X	detritivore
Insecta	Psocoptera	Trogiidae	X		detritivore
Insecta	Siphonaptera	Ceratophyllidae	X	X	parasite
Insecta	Thysanoptera	Thripidae		X	herbivore
Insecta	Thysanura	Lepismatidae: *Lepisma*	X	X	detritivore
Malacostraca	Isopoda	Armadilliidae	X		detritivore
Malacostraca	Isopoda	Porcellionidae	X		detritivore